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A COMPARATIVE MORPHOMETRIC STUDY OF THE HOMINOID LUMBAR SPINE

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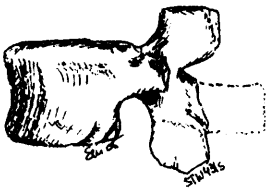
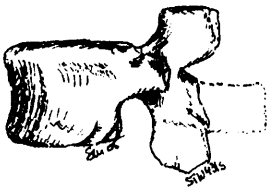
The fact of evolution is the backbone of biology, and biology is thus in the peculiar position of being a science founded on an improved theory - is it then a science or faith?

Charles Darwin (1809-1882)



To my parents Katharina and Renato Martelli. Without your support and enthusiasm this thesis certainly would not never have happened – thank you for everything

To the Memory of my good friend Brian Ruth. I wish you where still here to celebrate "The great disturbance in the Force"



ABSTRACT

This thesis investigates the size/shape variation in the lumbar spine of extant and fossil hominoids. As a novelty, 3D coordinate data sets were obtained from the last five consecutive presacral vertebrae for comparative analyses. Size/shape variation of single vertebrae and patterns of metameric size/shape variation along the lumbar spine are investigated. Large samples of populations of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus* are investigated. The fossil sample includes *Australopithecus afarensis*, *Australopithecus africanus*, and *Homo ergaster*. Statistical shape analysis was conducted using geometric morphometric methods. Comparison 1 (Chapter III) explores sexual dimorphism in size and shape within each of the modern taxa. Results indicate that *Pan* shows neither vertebral size nor shape dimorphism. *Gorilla*, and probably *Pongo* (small sample size) are highly sexually dimorphic in size and less so in shape. *Homo sapiens* shows less size dimorphism than *Gorilla* but a markedly larger shape dimorphism. Thus despite sexual dimorphism of locomotor repertoires within great apes there are few indications of these in vertebral shape. In contrast, humans with no dimorphism in locomotor repertoire, show shape dimorphism in the lumbar spine related to sexual differences in pelvic shape and consequent differences in bipedal kinematics. Comparison 2 (Chapter IV) investigates inter-specific size/shape variations between extant hominoids. It is found that differences in shape between the taxa corroborate the functional relationships already described in the literature. Further, the differences between the taxa in shape are not congruent with the consensus molecular phylogeny. Comparison 3 (Chapter V) focuses on the fossils. Results indicate that *A. africanus* and *A. afarensis* lumbar vertebrae are most similar to each other. In comparison with modern taxa, they are most similar in shape to those of modern humans and less so to great apes. *Homo ergaster* falls within the range of modern humans. This thesis concludes that lumbar vertebral morphology shows interesting intra-specific patterns of scaling and of sexual dimorphism that appear to vary according to function between apes and between apes and humans. The australopithecines show similarities in shape with modern humans, indicating that despite inter-specific differences in pelvic shape, there are key adaptations in the lumbar spine which guarantee an energetically efficient bipedalism that was developed as early as 3 million years ago in the hominin lineage. However, humans and australopithecines differ in that the latter show no adaptations in the vertebral column to bipedal endurance running. Chapter VI concludes with a protocol for the analysis of future fossil vertebral discoveries.

ACKNOWLEDGEMENTS

I am very grateful to my supervisors Paul O'Higgins and Christopher Dean for their guidance, advice, encouragement and inexhaustible patience. Without their ongoing efforts, this thesis could not have happened. I would also like to thank Paul O'Higgins for the tremendously enjoyable and fruitful scientific discussions taking part over the years and for reading the manuscript and the constructive remarks and criticism thereof.

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reconstructing the CT data, how to use the software suite amira™ and who also generously helped with the production of the CT scan images shown in the appendix.

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Last, but not least, my heartfelt thank goes to everybody who in any way (no matter how unorthodox) has contributed to the making of this thesis even if they cannot all be mentioned here by name.

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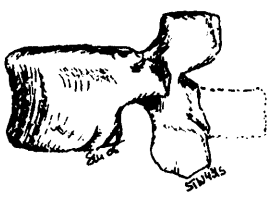

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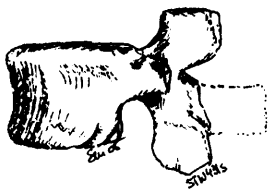


CHAPTER I INTRODUCTION

1.1 Introduction

Bipedal walking and bipedal running are considered major steps in the evolution of hominins and modern *Homo sapiens*. These go together with increased encephalization, tool production (including use of fire) and the development of language. All these steps did not evolve simultaneously but in a mosaic-like manner and the interaction and dependencies of these traits are manifold. Since bipedal walking gait is likely the first of these to have evolved, it is of great importance to understand its origin in terms of the skeletal morphology linking living and fossil hominins and how the necessary adaptations emerged within the hominid lineage.

It is not only important to know which hominin taxon actually engaged in habitual bipedalism (which, in this thesis, principally refers to bipedal walking) as part of their locomotor repertoire, but an understanding of the biomechanics of bipedal gait and the proportion of the total locomotor repertoire devoted to it is crucial to give us valuable insights into how and why bipedalism evolved in the hominin lineage.

To investigate the anatomical basis of bipedalism, it is necessary to study the postcranial skeleton. Of this, the axial skeleton forms the framework for the motions which propel an animal forward. With regard to the function of the axial skeleton in locomotion, Gracovetsky (1985) considers the lumbar spine to be *"the key element in land locomotion of mammals"* and the size and structure of lumbar vertebrae to be highly correlated with locomotor behaviour in terrestrial mammals. The shape of the lumbosacral complex mirrors the locomotor modes a species normally engages (Boszczyk et al., 2001; Slijper, 1946). This has been documented for the modern human spine and pelvis which are highly adapted to our unique bipedal gait (e.g. Gracovetsky 1985). However, with regard to the differences between modern humans, fossil hominins and recent African great apes an understanding of how differences in the morphology of these bones are related to function is not yet complete. Also, the extent to which fossil hominids were habitual bipeds and what style of bipedal gait (chimpanzee-like, modern human-like or unique?) they engaged in is a matter of ongoing debate that will be examined at a later stage of this review.

Differences in the morphology of the lumbosacral complex and the pelvis of humans, great apes and fossil hominins are therefore of particular interest because they might help to reveal how the habitual bipedal gait of modern humans has evolved. In this regard the human spine, especially its lumbar section – together with the pelvis - can be considered highly specialized in both anatomy and function. This is because of all the extant primates, humans are the only habitual bipeds and this unique form of locomotion has resulted in some very specific adaptations, particularly in the pelvic girdle and lower limbs. Compared to the upper limb, the lower limb of *Homo* has undergone considerable transformation and adaptation. This makes sense, since the lower limb exclusively has contact with the substrate on which locomotion is performed in bipedalism. An important argument, as to why the focus of this thesis is mainly on the spine and its lumbar segments is that the spine and especially the lumbar segments are crucial structures in mammalian terrestrial locomotion in maintaining, providing and controlling the transformation of potential into kinetic energy during locomotion. As such, knowledge about the relationship between structure and function of the spine of our hominin ancestors as well as extant closest relatives is central to our understandings of the origins of bipedalism.

As will be discussed throughout this chapter, there is disagreement about the locomotor repertoire displayed by the Plio-Pleistocene hominin taxa. It has been suggested that more "recent" species, e.g. *Homo erectus* and *Homo neanderthalensis* were fully bipedal and that this is reflected in the shape of their vertebral column and pelvis (Ruff and Walker, 1993; Shackelford and Trinkaus, 2002; Stringer and Gamble, 1993; Trinkaus and Ruff, 1999a; Trinkaus et al., 1999). Nevertheless, in the case of *Homo erectus*, although considered fully bipedal, there is dispute about the length of the lumbar spine and the consequences of this on the biomechanics of *Homo erectus* (Walker and Leakey, 1993).

In the case of australopithecines, differences in opinion arise about how "human"-like australopithecine vertebrae are. Represented by specimens Sts14 and Stw431, the lumbar spine of *Australopithecus africanus* may have most likely been adapted to bipedal gait but one cannot be sure about this. Adaptations to bipedalism as seen in modern humans have either not been described fully or interpreted differently. It also has not been considered, that –if *Australopithecus africanus* was a bipedal taxon – the lumbar spine in Australopithecine might have been adapted to different bipedalism biomechanics since

there seems to be evidence that the shape of the pelvis, femur and the muscle attachments to these are different, both from great apes as well as humans. This indicates that australopithecines could have been bipedal but with a different biomechanics than modern humans. If so, this might be traced in the shape of the lumbar spine.

There is also a considerable debate about the locomotor affinities of *Australopithecus afarensis*. Despite the findings of the Lateoli footprints, traditionally associated with *A. afarensis*, there is strong evidence that its postcranium – especially the upper limbs –was well adapted to arboreal locomotion. Their locomotor repertoire might have included a different proportion of bipedalism compared to *A. africanus,* and maybe different biomechanics since they also differ somewhat in the morphology of their feet, knee joints and pelves, as well as in their body proportions. In any case, the australopithecine postcranium seems to lack specific adaptations to endurance running as seen in modern humans (Bramble and Lieberman, 2004). In general one can say that there is no clear consensus as to how these taxa resemble each other, and in what way their locomotor repertoire is reflected in the shape of their spine. Also, there is dispute about the locomotor repertoire within the taxon *A. africanus* since the two specimens known from partial skeletons seem to differ quite substantially in size (Häusler and Schmid, 1995; McHenry, 1991b) and body proportions e.g. McHenry and Berger (1998). How this influences the shape of the vertebral column is not yet clear. Additional knowledge about the postcranial regions of australopithecines which underwent considerable remodelling in the human lineage, e.g. feet, legs, pelvis, and the lumbar spine might help to clarify such issues.

1.2 The importance of geometric morphometrics

The anatomy of different primate taxa, both fossil and recent has been studied by qualitative and quantitative analyses. Most early studies of comparative anatomy utilized a qualitative approach, where the aim was to describe anatomical structures and to discuss the presence or absence of particular features or the differences in orientation and prominence of anatomical structures. Such studies provided the framework and basis for comparative anatomy and morphology as well as palaeontology. However, the downside was that these studies usually only examined small sample sizes. Hence they were rather subjective and the loss of information about variation of morphology was considerable. The latter is an important factor when dealing with fossil material. Since

fossil specimens – especially in case of hominin taxa – are rare, researchers have to base their studies on the assumption that the fossil specimens are adequate representations of their taxon. To quantify this, the intra-specific variation within the closest related living taxa can be utilized as a comparative measure. This leads to the requirement to quantify morphology using large samples of extant taxa that can be objectively measured. Thus, fossil taxa can then be compared using suitable statistical techniques.

The traditional way of doing this used to be through quantitative analysis of distances and angles measured on the relevant skeletal elements. Often, these measurements or combinations thereof are converted into indices allowing statistical analyses of proportions (shape).

The fundamental advances of geometric morphometrics over traditional approaches are in the development of powerful statistical methods designed for analysis of shape data represented by the co-ordinates of landmarks themselves rather than the use of standard multivariate methods on ad hoc collections of distances, angles, and ratios between landmarks (O'Higgins, 2000; Rohlf, 2000a; Rohlf, 2000b). Geometric morphometrics and modern computers allow three-dimensional data analysis and representation of large data sets as well as the visualisation of complex three-dimensional structures such as vertebrae with the several processes attached to them e.g. (Bookstein, 1991; Dryden and Mardia, 1998; O'Higgins, 2000; O'Higgins and Jones, 1998). The statistical powers of various alternative morphometric methods and visualisation that lead to the choice of geometric morphometric analyses employed for the studies presented in this thesis will be elaborated in Chapter II, materials and methods.

The comparative anatomy of the hominin spine has been of interest in the past, however, only a few quantitative analyses have been carried out. All have used the traditional approach and, to date, there has been no attempt to address the morphological affinities and subsequent function of fossil hominins using the geometric morphometric approach.

1.3 Objectives of this thesis

In this study, variations in size and shape of single lumbar vertebrae and patterns of vertebral size and shape variation along the lumbar spine will be assessed within and between modern and fossil hominoid taxa. The relationships between vertebral size and shape variation and factors such as intra – and inter-specific differences in body weight, locomotor repertoires, and phylogeny will be explored. Fossil taxa will be compared to modern humans, recent African great apes, and recent Asian great apes in order to investigate trends and events in human evolution concerning the evolution of bipedalism. The approach used will be geometric morphometric three-dimensional shape analysis. The following list summarizes the objectives of this thesis:

1. To assess the presence of sexual dimorphism in lumbar vertebral size and shape within modern hominoid taxa (*Homo sapiens, Gorilla gorilla, Pan troglodytes*, and *Pongo pygmaeus*)
2. To investigate the relationship between lumbar vertebral size and shape dimorphism and sexual dimorphism in body weight within each of the modern hominoid taxa
3. To assess the extent to which patterns of inter-segmental vertebral shape variation along the lumbar spine differ between the sexes of the four modern hominoid taxa
4. To assess how sexual dimorphism in vertebral size and shape is established throughout postnatal ontogeny in modern hominoid taxa
5. To confirm and assess inter-specific differences in lumbar vertebral size and shape between the modern hominoid taxa
6. To investigate inter-specific lumbar vertebral size and shape variations in relation to inter-specific differences in body weight, inter-specific differences in locomotor repertoire and phylogenetic history
7. To assess the extent to which the patterns of inter-segmental shape variation along the lumbar spine differ between the modern hominoid taxa in the study and how these differences are established throughout postnatal ontogeny

These objectives provide the framework for the comparison of modern hominoid taxa with fossil hominins (*Australopithecus* and *Homo ergaster*). The aims of the study, regarding the investigation of the fossil hominin samples is as follows:

8. To consider australopithecine lumbar vertebral size and shape variation in relation to that found previously in the modern hominoid taxa
9. To assess the differences in lumbar vertebral size and shape and differences in vertebral size and shape variation patterns between the fossil hominin taxa *A. africanus*, *A. afarensis,* and *Homo ergaster* and the modern taxa *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes,* and *Pongo pygmaeus*
10. Finally, to relate differences in vertebral size and shape variation between fossils and between fossils and modern taxa to currently held views on the fossil hominin locomotor repertoires

1.4 Structure of this thesis

The present chapter (I, Introduction) reviews the literature relevant to the evolution of the modern human spine and the evolution of bipedalism in hominin taxa. Section 1.5 introduces the anatomical and taxonomic terminology used throughout the present study. Section 1.6 discusses the role of the mammalian vertebral column in locomotion and the biomechanics of the human lumbar spine in relation to upright bipedal gait. This is followed by section 1.7, which then introduces the different locomotor repertoires of the great ape taxa. Section 1.8 discusses the comparative context of fossil hominin spinal remains. Section 1.9 addresses the comparative anatomy of the spine of extant hominids with emphasis on the regionalization and variation in the numbers of vertebrae in the hominid taxa represented in the study. Finally, section 1.10 reviews briefly the genetic signalling which orchestrates the development of the axial skeleton and the lumbar spine in particular as far as is known to date.

Chapter II (Material and Methods) discusses and introduces the recent and fossil materials. It describes the reconstruction of fossil vertebral material, methods of data collection and introduces geometric morphometric methodology. The statistical procedures employed to analyse data are presented as well.

In Chapter III (Intra-specific lumbar vertebral size and shape variation) aims 1 to 4 (see previous page) are investigated. Thus, sexual dimorphism in vertebral size and shape within the modern hominoid taxa is studied. Hypotheses are formulated to be tested for the presence or absence of a significant relationship between differences in vertebral

size and shape and sexual dimorphism in body weight. Addressing aim 4, the postnatal ontogeny of vertebral size and shape variation is also explored.

Chapter IV (Inter-specific lumbar vertebral size and shape variation) addresses aims 5 to 7 and therefore assesses inter-specific differences in vertebral size and shape between the modern hominoid taxa. Hypotheses are formulated to test for significant relationships between inter-specific differences in vertebral size and shape and inter-specific differences in body weight, locomotor repertoires, and phylogeny.

Chapter V, addresses aims 8 to 10 and investigates the vertebral size and shape variation within australopithecines as well as between australopithecines and between australopithecines and modern hominoid taxa. The results from these assessments are then related to the currently agreed hypothetical locomotor repertoires of fossil taxa.

Chapter VI, finally, brings together the different results from Chapters III, IV, and V and attempts to interpret them in view of the topics discussed in Chapter I so that a number of conclusions about hominid locomotor evolution can be drawn.

1.5 Background

1.5.1 Notes on general terminology

In the following sub-chapters, the terminology, both functional and anatomical, is introduced in order to establish usage throughout this thesis:

1.5.2 Definitions of hominoid taxonomy

Throughout the thesis, the following taxonomic nomenclature will be used (see figure 1.1) This nomenclature has recently been promoted as the most appropriate in classifying not only recent but also fossil taxa (Wood and Richmond, 2000). This nomenclature is in contrast to a "pre-molecular" classification of primates (Linné, 1758), adapted by (Simpson, 1931) where the African apes formed a group separated from modern humans. The current nomenclature takes into consideration results of various studies which support a closer relationship between *Homo sapiens* and *Pan* than between *Pan* and *Gorilla*. Molecular data from the study of proteins and mitochondrial

DNA (Gagneux et al., 1999; Ruvolo et al., 1991; Ruvolo et al., 1994) seem to support this. Nonetheless, one should keep in mind that some researchers, based on the close morphological resemblance of the African great apes are sceptical about the current interpretation of the molecular data. In addition they stress that the molecular data separating the *Homo-Pan* clade from *Gorilla* is not entirely convincing (Andrews and Martin, 1987), particularly in the face of the fossil record. However, since to date most studies support the *Homo-Pan* clade, this view will be adopted in the present study. Further research in molecular biology will be necessary to resolve the issue of phylogenetic distance within the African ape – human clade.

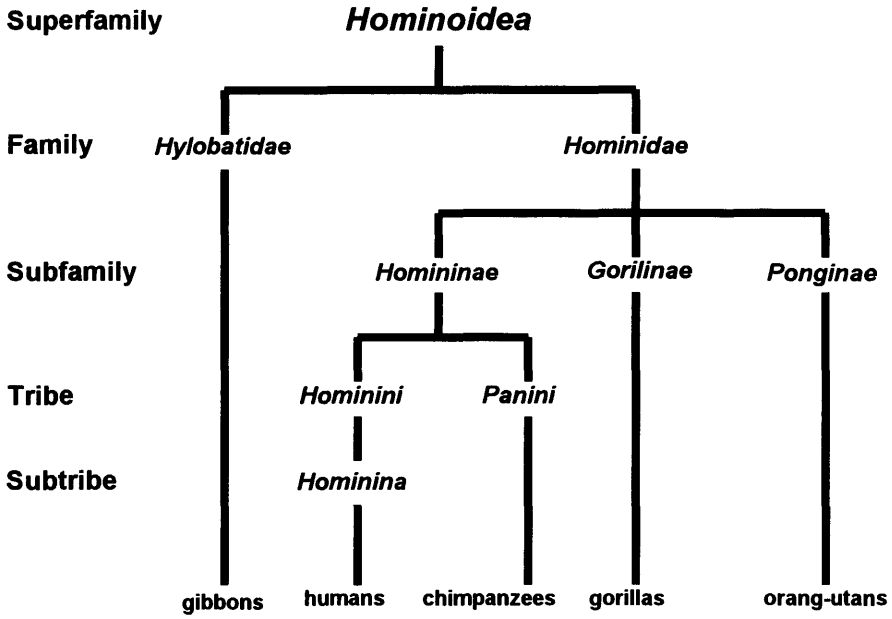


Figure 1.1 Taxonomy of modern hominoids, after Wood and Richmond (2000a). It takes into consideration the small genetic distance between *Pan* and *Homo*. "Branch length" is not consistent with phylogenetic distances

For easier reading, taxonomic terms are used mostly in their common English form throughout this thesis as suggested by Wood and Richmond (2000b). Where it is considered to be necessary for the sake of clarity to use the Latin terms, these are written in Italics. Terms used throughout this thesis are as follows (Wood and Richmond, 2000):

Hominidae	hominids	*Homo*, *Pan*, *Gorilla*, *Pongo* and *Australopithecines*
Homininae	hominines	(*Homo*, *Pan*, and *Australopithecines*)
Hominini	hominins	(*Homo* and *Australopithecines*)
Hominina	hominans	Genus *Homo*

1.5.3 Terminology of locomotion

Throughout the thesis, the terms "locomotion", "locomotor mode", and "locomotor repertoire" will be used extensively. Their definitions are listed here.

Locomotion	This term describes the ability of active motion.
Locomotor mode	This term is used as a substitute for locomotor activity and describes a particular type of locomotion. In primates, this will be e.g. climbing, walking, running or leaping and others.
Locomotor repertoire	The locomotor repertoire describes the entire range of locomotor modes which are used by a particular taxon. For example, the locomotor repertoire of humans consists of only two locomotor modes - bipedal running and walking – whereas the locomotor repertoire of African apes consists of quadrupedal walking, climbing and suspensory behaviour etc.

1.5.4 Translation and use of Latin anatomical terminology

Throughout this study, the formal Latin anatomical terms will be replaced by their English translations for easier reading. The list below introduces the most commonly used Latin terms and their English translations.

Corpus vertebrae	vertebral body
Lamina vertebralis	lamina
Processus articulares superiores et inferiores	superior/inferior articular processes
Facies articulares superiores et inferiores	superior/inferior articular facets
Processus costales	costal processes
Processus spinosus	spinous processes

Processus accessorius	accessory processes
Processus mammillaris	mammillary processes
Canalis vertebralis	vertebral canal
Incisura vertebralis major	same
Incisura vertebralis minor	same

When mentioned in the text, the terms for muscles and other anatomical terms which are used infrequently are in the Latin form and highlighted in Italics.

A note to the use of the term "costal process": In accordance with *Nomina anatomica*, transverse processes are called costal processes throughout the study. This is because in the lumbar region, the morphological equivalents of the transverse processes of the thoracic vertebrae are actually the accessory processes. The laterally projecting processes of the lumbar vertebrae are formed by the rib-anlage of thoracic vertebrae and are officially called costal processes. Since this study concentrates exclusively on lumbar vertebrae it seemed appropriate to use the term costal process.

1.5.5 Anatomical orientation

Throughout this thesis, descriptions of differences in vertebral shape are frequently described in relation to the orientation of the whole organism. However, these terms vary between a pronograde (apes) and orthograde (humans) positioned organism. Thus, terms of anatomical orientation used throughout the thesis follow the definitions presented in figure 1.2 (Ankel-Simons, 2000).

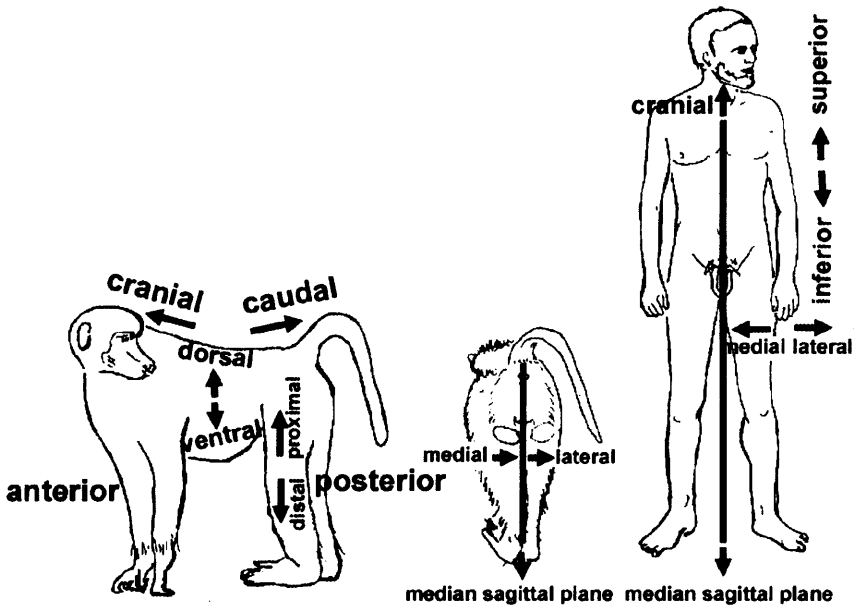


Figure 1.2 Anatomical orientation of pronograde and orthograde bodies. Modified from Ankel-Simons (2000), p. 250

Confusion sometimes arises from the use of the terms "length", "width", and "height" in order to describe the dimensions of the vertebral body. This is most likely because the terms refer to pronogradally orientated vertebrae (as seen in quadruped vertebrates). To avoid any confusion, the following figure 1.3 clarifies the use of these terms in this thesis.

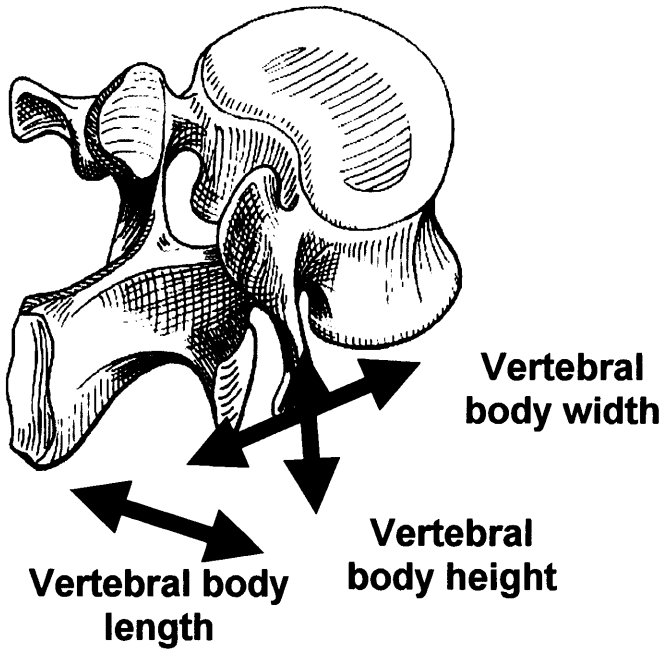


Figure 1.3 Definition of vertebral body length, height, and width in a modern human lumbar vertebra. Modified from Kapandji (1982), p. 69

1.6 The role of the mammalian vertebral column in locomotion

The role of the mammalian vertebral column in locomotion is twofold: it provides maximum stability to maintain the shape of the trunk and the body in general (load bearing) and simultaneously maintains maximum mobility of the trunk (shock absorption and energy efficiency (Badoux, 1974; Boszczyk et al., 2001; Gracovetsky, 1986; Slijper, 1946). Additionally, it also protects and maintains the integrity of the neural structures.

In terrestrial quadrupeds, the orientation of the body axis usually reflects a compromise between the (vectoral) directions of gravitational forces (body weight support) and propulsive forces generated by the hindlimbs and transmitted to the forelimbs during locomotion. The vertebral column must also be able to resist deforming loads and to absorb impacts from propulsive forces (e.g. shock absorbance transmitted from ground through limb to vertebral column when feet make contact with the substrate during locomotion) (Badoux, 1974; Boszczyk et al., 2001).

Mammalian trunk morphology has been compared to a "bow and string" construction in which the "bow" consists of the vertebral column whereas the string represents the dorsal and ventral muscle groups which flex and extend the vertebral column (see figure 1.4). In this model, the relative stiffness of the mammalian thoracolumbar spine necessary to lift the body off the ground is best explained. The elasticity of the vertebral column (rod) is derived from the *Annuli fibrosi* of the intervertebral discs and the ligament apparatus. The dorsal muscle group (string) consists of the *Erector spinae* which extend the spine. There are two ventral muscle groups. The first group comprises the pre-vertebral muscles of the cervical, upper thorax, and lumbosacral region (*Longus colli*, *Longus capitis* and the *Psoas* group). The first group is the main flexor of the spine. In conjunction with the extensors, the first group stabilizes the spine. The second group primarily flexes the spine in the thoracolumbar region and is important in spinal flexion and extension during bounding locomotion. The second group consists of *Transversus abdominis*, *Obliquus externus* and *internus*, and *Rectus abdominis*. Some of these muscles also play an important role in lateral bending and rotation of the trunk (Badoux, 1974; Slijper, 1946).

According to Boszczyk et al. (2001), Gracovetsky (1986), and Slijper (1946) the lumbar section of the vertebral column is subjected to the most extensive and diverse strain

patterns in relation to weight support and locomotor functions. This is because most mammal taxa produce propulsion forces with their hindlimbs. Differences in lumbar vertebral shape between species are therefore highly likely to be related to differences in inter-specific differences in locomotor repertoires.

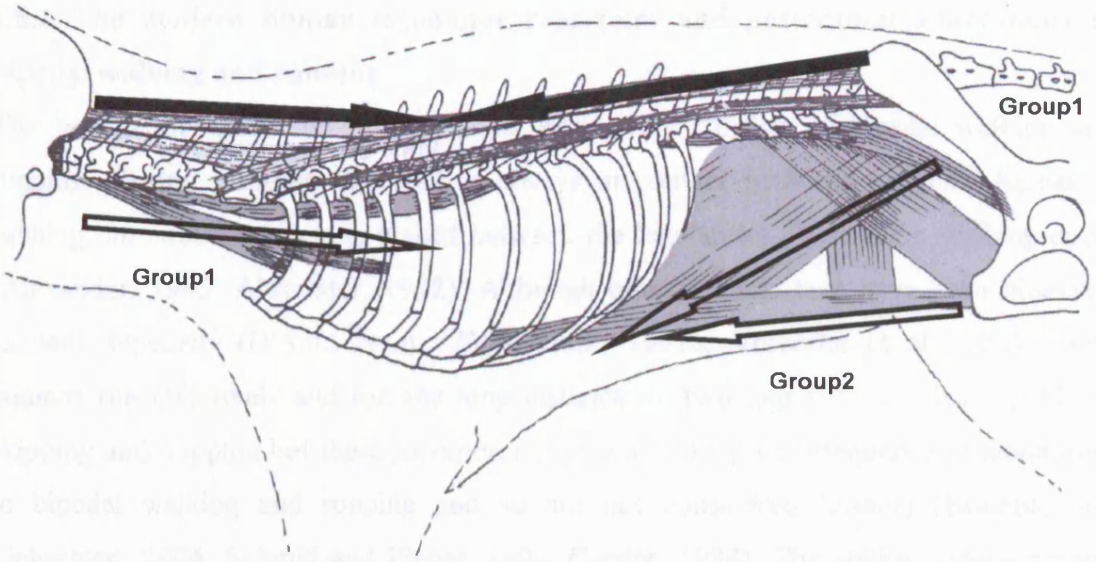


Figure 1.4 "Bow and string" spine model of the terrestrial quadruped mammal. Light grey muscles belong to the dorsal extensor group, dark grey ones to the ventral flexors. Black arrows indicate direction of actions of extensors, white arrows the direction of action of flexors. For explanation of action of groups 1 and 2 see text above. Adapted from Badoux (1974), p. 12

Due to their upright bipedal gait, the vertebral column of modern humans differs from most mammals in that their vertebral column performs the same functions but is rotated by 90°. Nevertheless, as in other mammals, the human lumbar spine plays a crucial role in transmitting propulsion forces since these are produced by the hindlimbs during locomotion (Gracovetsky, 1985; Gracovetsky, 1986; Slijper, 1946). As in most mammals, the human lumbar spine therefore shows considerable flexion-extension motion during locomotion. Additionally, the human hip-pelvic-lumbar spine complex performs considerable lateral bending during locomotion. This motion plays a role in the transformation of potential into kinetic energy during locomotion which guarantees an energetically efficient and smooth stride during walking and running. In the following sections, the human locomotor repertoire and the biomechanics of the human

bipedal walking gait are introduced. Bipedal walking is extensively covered because it was present in early fossil hominins yet bipedal running most likely was not (Bramble and Lieberman, 2004). However, in section 1.6, a brief introduction into differences in bipedal running and walking is presented.

1.6.1 The modern human locomotor repertoire and postcranial adaptations to bipedal walking and running

The human locomotor repertoire almost exclusively consists of bipedal walking and running. During walking, one foot is always in contact with the ground whereas in running, an airborne phase is placed between the heel-strike phases of a walking cycle (Alexander, 1985; Alexander, 1992). Although other primate taxa have been observed to walk bipedally (D'Aout et al., 2004; Hunt, 1991b; Vereecke et al., 2003), only humans run effectively and for any long distance on two legs (we are also capable of skipping and hopping but these locomotor modes are likely a consequence of adaptation to bipedal walking and running and so are not considered further) (Bramble and Lieberman, 2004; Schmid and Piaget, 1994, Carrier, 1984). The ability (unique among primates) to perform well in long distance endurance running makes modern humans comparable to open habitat quadrupeds such as e.g. zebras or hunting dogs (Bramble and Lieberman, 2004; Carrier 1984). The human postcranium is highly adapted to these bipedal locomotor modes. The hindlimbs are long and rather large (Napier and Napier, 1967; Schultz, 1933). The knee joints and hip joints are large (Jungers, 1988; McHenry, 1991a) and provide the only support of the body weight under high force impact. The pelvis is short and broad and has evolved an effective "bowl-shaped" support for the intestines to be carried and the spine is robust for better supporting the bodyweight resting on it. It is also curved for better shock absorption (Alexander, 1992; Fleagle, 1976; Harrison et al., 1977; Napier, 1967; Schultz, 1931). In modern humans, bipedalism is acquired during postnatal ontogeny. First attempts at walking start around the age of 10 to 18 months. These attempts become more adult-like in terms of stride frequency, phase swinging, and heel-strike, between the age of 50 to 90 months (4 to 7 years) (Vaughan et al., 2003). Before the age of 10 months, humans engage in other forms of "locomotion", of which crawling is the most frequent.

1.6.2 The modern human spine in bipedal locomotion

In comparison to the great ape lumbar spine (presented in the sub-chapters addressing the role of the lumbar spine in great ape locomotion later in this chapter), the human lumbar spine is more flexible and weight transmission mechanisms differ widely. Differences in weight transmission mechanisms through the lumbar spine between modern humans and great ape taxa are highly likely related to the difference in direction in which compressive loads are acting on the lumbar spine of humans and great apes during walking and running. Figure 1.5 further illustrates the difference in direction of loads between humans and (African) great apes.

The differences in load transmission through the vertebral column are due to differences in habitual trunk posture during locomotion between great apes (predominantly pronograde) and modern humans (exclusively orthograde). Due to the habitually orthograde trunk posture of modern humans, their lumbar spine (and the vertebral column as a whole) is predominantly exposed to vertically compressive loads and torsion (Adams and Hutton, 1983; Boszczyk et al., 2001; Krismer et al., 1996). These loads vary continuously during bipedal standing, and locomotion.

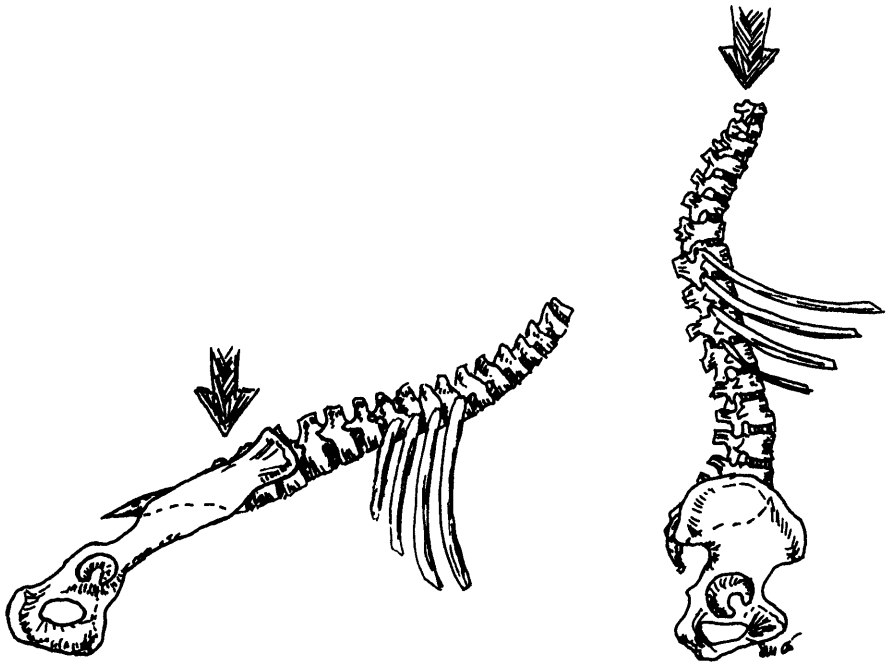


Figure 1.5 Weight transmissions through the chimpanzee and human lumbar spine. In humans, trunk support predominantly rests on the lumbar spine. Note the "compromise" orientation of the great ape pelvis: it guarantees optimal weight support whilst providing maximal leverage for hip extensors (attachment on ischial tuberosity). Arrows indicate differences in axial loading in humans and great apes. After Schultz (1957), p. 346

The greater mobility of the human vertebral column (when compared with great apes) is highly likely to be related to shock absorbance during bipedal gait. Further, the mobile human lumbar spine facilitates the dynamic equilibrium necessary to balance the vertebral column over the hip joints with minimal energy costs. Humans have an elaborate spinal ligament system which supports the upright trunk and keeps the spine aligned upright (Adams and Hutton, 1983; Gal, 1993; Jemmett et al., 2004; Papp et al., 1997). Nevertheless, small muscle movements and flexibility in the spine are needed to constantly adjust and correct the trunk position in equilibrium over the pelvis. For these reasons, humans have the most mobile and also the longest (relative to vertebral body length and with regards to vertebral numbers) spine among the hominoid primates (Schultz, 1931; Schultz and Straus, 1945).

In the following sections a brief introduction of the role of the lumbar spine in human bipedal locomotion is presented. Topics covered consist of load transmission mechanisms of the human lumbar spine, the motion of the lumbar spine during locomotion, and transformation of elastic and kinetic energy in the vertebral column during locomotion. Since the best way to describe the mechanism of human bipedal walking is to describe a walking cycle and the role of the spine in it, this will be done in the following paragraphs.

1.6.3 Architecture of the vertebral column and the spine as a whole in its role of resisting compressive forces and their transmission

The main load acting on the human spine is axially orientated due to the spine's upright position. The spine as a whole, therefore, is optimally adapted to resist compression loads. Thus, the size of the vertebral bodies gradually increases towards the last lumbar elements, indicating that towards the sacrum, more and more weight is borne by them (Davis, 1961; Odgers, 1933; Pal and Routal, 1987).

The two column model

The vertebral bodies are not solely responsible for the transmission of compression forces. A part is transmitted through the vertebral arches and the zygapophyseal joints (Davis, 1961; El-Bohy, 1989; Pal and Routal, 1987). Pal and Routal investigated the function of the vertebral arch and the zygapophyseal joints in force transmission. They found that in the thoraco-lumbar region, a two-column model best describes the way the

spine resists compressive forces. The first column consists of the vertebral bodies and intervertebral discs and the second consists of the vertebral arches and zygapophyseal joints. As there is more body weight supported the further down the vertebral column a vertebra is positioned, the second column contributes more and more to the weight bearing, thus the vertebral arches become stouter towards the caudal end of the presacral spine (Pal, 1989; Shapiro, 1993a). The bone of the vertebral arch and pedicles is dense and provides optimal resistance against the large compression forces that must be accommodated during motion of the spine. The pedicles play an important role in transmitting forces from the one weight bearing column to the other (Pal and Routal, 1987; Taylor, 1984). In the thoraco-lumbar region, the transmission of force between the two columns is mostly from the first to the second column (this in contrast to the cervical spine and upper thoracic one, where the transmission of forces from one column to the other mostly happens from the second to the first column (Pal and Routal, 1987). Transmitting forces between the two columns increases shear stress and torsion between the columns. The pedicles are therefore adapted to resist these forces, as are the zygapophyseal joint facets (Cihak, 1981; El-Bohy, 1989). In the second column, the zygapophyseal joints have a similar role is the intervertebral discs in the first column: in terms of kinematics, they constrain the movement of neighbouring vertebrae and they transmit forces (mainly compressing ones) (Bergmark, 1989) and increase the mobility of the second column, which in humans is crucial as we will see later in this chapter.

Internal bone architecture

Adaptations to weight bearing and load transmission are also expressed in the internal bone architecture of the lumbar vertebrae. The macroscopic structure of bone consists of a dense, external layer, the cortical bone, and a less dense, internal cancellous bone, the trabeculae. This design of a strong and stiff surface material with a weaker and more flexible interior results in a composite structure that is strong for a given weight (Knudson, 2003). Bone is known to remodel to optimise its structure according to its mechanical environment. It emerges that selected aspects of the internal architecture of the bone, such as the distribution of anisotropic and isotropic trabeculae, provides a useful tool to conduct inter-specific comparisons between primates showing different modes of locomotor adaptation (Buck et al., 2002; Fajardo et al., 2002; Ryan and Ketcham, 2002; Yang and Oxnard, 1979). It has been shown that based on studies of the internal bone architecture of vertebrae, it is possible to discern differences in locomotor modes between different taxa. Studies by Mitton et al. (1998) show that the internal

bone architecture of vertebrae differs significantly between humans and sheep and that these differences are most likely related to differences in compressive forces and shear stress caused by differences in loading patterns of the spine. In another study, Brown et al. (2002) compared the cancellous bone structure of the lumbar vertebrae in humans, chimpanzees and a Neanderthal fossil (Kebara II). Both, modern humans and Neanderthal were found to be similar in showing adaptations to a lumbar lordosis and vertical compressive loads, while the more isotropically orientated trabeculae of the chimpanzee vertebrae departed from that pattern.

Intervertebral discs

The intervertebral discs transmit loads between neighbouring vertebral bodies and control motion between them. In the lumbar spine, the discs are posteriorly wedge-shaped and contribute considerably to the degree of lumbar lordosis (Gracovetsky, 1985; Gracovetsky, 1986). The intervertebral disc is composed of three parts; the endplates, the *Annulus fibrosus*, and the *Nucleus pulposus*. The *Annulus fibrosus* is a ring-shaped structure composed of concentric layers of collagen fibres. The fibres of each layer are arranged in differing directions between neighbouring layers, see figure 1.7.

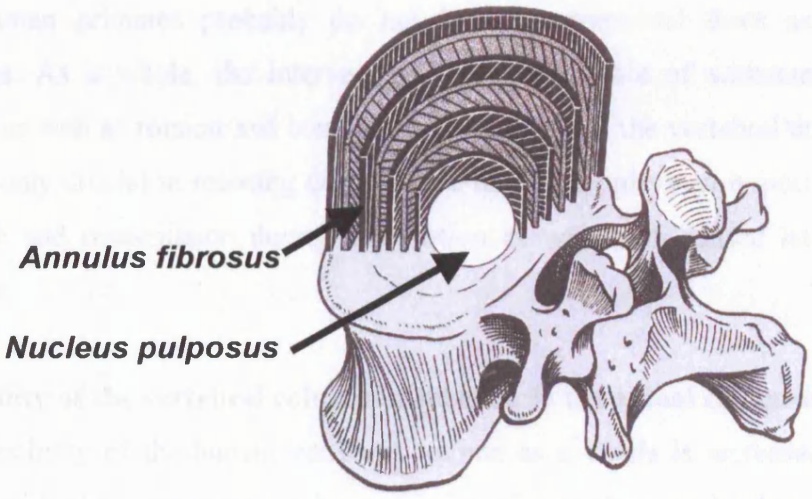


Figure 1.6 Anatomy of the intervertebral disc. Note that orientation of fibre layers alternates in the *Annulus fibrosus*. The *Nucleus pulposus* is shown in its spherical unloaded shape. Adapted from Kapandji (1992), p. 26

The layers are bound together and prevented from buckling by a matrix of proteoglycan gel (Kapandji, 1992). The layers of collagen fibres of the *Annulus fibrosus* are alternatingly tightened and loosened when rotation is applied to the spine. Thus the

Annulus fibrosus is crucial in withstanding torsion forces applied or removed. Recent studies indicate that the *Annulus fibrosus* can resist higher loads of torque force than the joint facets (Krismer et al., 1996). The *Nucleus pulposus* is a gel-like spherical mass, in the central portion of the disc. It is always under pressure and exerts a preload to the disc (Kapandji, 1992). The *Nucleus pulposus* is well suited for withstanding compressive forces applied to the motion segments.

Another worthwhile observation is the fact that the human intervertebral discs are thick which increases the mobility between two vertebrae. The absolute average height of a human lumbar intervertebral disc is 9 mm (Kapandji, 1992). It is more difficult to decide if that is a lot in comparison to non-human primates since data on absolute intervertebral disc height of non-hominoid primates are not available. However, measurements of lumbar intervertebral disc heights in transverse and coronal sections of an adult (male) chimpanzee, stored in the animal collection of University College London revealed that the average absolute height of lumbar discs in chimpanzees range from 6.5 to 7 mm for discs between vertebrae from L1 to L4. The disc between L4 and S1 measures 4.8 mm on average. These numbers are based on the measurements of only one animal and are therefore to be used with great caution. But they can indicate that non-human primates probably do not have intervertebral discs as tall as those in humans. As a whole, the intervertebral disc is capable of withstanding compressive forces as well as torsion and bending forces applied to the vertebral column. This ability is not only crucial in resisting compressive forces but plays an important role in energy storage and transmission during locomotion as will be discussed later in the relevant chapter.

Flexibility of the vertebral column in relation to the spinal curvatures

The flexibility of the human vertebral column as a whole is increased by its unique s-shape with three curvatures; the cervical lordosis, thoracic kyphosis and the lumbar lordosis. This configuration reduces its longitudinal stiffness (Adams, 1985). The curvatures of the spine are clearly an adaptation in relation to locomotor function. The spine of newborn humans has no distinctive curves save for a general ventral curvature, which gives it a C-shaped appearance. The first curvature to be established is the lordosis of the cervical spine, followed by the thoracic kyphosis and the lumbar lordosis which develop around the age of 13 months. However this process is not completed until the age of 10 years. That the lordosis develops in consequence of the upright body

posture and bipedal gait has been demonstrated by Hayama et al. (1992). They investigated the lumbar spine of Japanese macaques (*Macaca fuscata*) which were trained to walk bipedally from a very young age onwards and were daily exercised for the duration of their lives. Radiographs of their vertebral columns revealed that a permanent lumbar lordosis had formed, which was maintained if the animal was standing pronograde on all four legs. However, in the same study, it was shown that this lordosis was not caused by changes in the vertebrae but was achieved by the intervertebral discs which adopted a posteriorly wedged shape.

1.6.4 Biomechanics of human bipedal locomotion

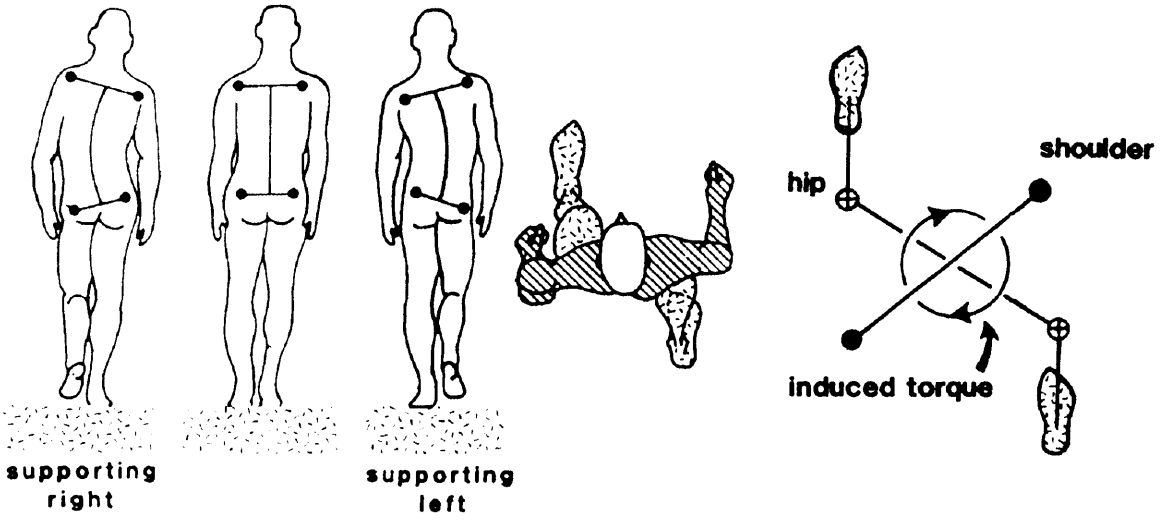
The coupled flexion-rotation motion of the spine

When whales returned to an aquatic lifestyle, they had to adapt from terrestrial to aquatic locomotion. In their biomechanics, they preserved the mammalian heritage of the flexion-extension motion of the spine instead of "re-adapting" to the lateral flexion motion of most aquatic vertebrates (e.g. fish). This mammalian heritage is not only preserved in the aquatic locomotion of whales – humans have just as well preserved the flexion-extension motion of the spine in bipedalism. Nevertheless, compared to other terrestrial mammals, there is a significant difference in that the flexion-extension motion is, compared to pronograde mammals, rotated by 90° due to the permanently erected vertebral column. In contrast to most mammals, during walking, the human spine not only flexes and extends in the sagittal plane, but also performs considerable lateral bending. Hence a coupled rotation-flexion motion of the spine results.

The human spine as inverted pendulum model

According to Gracovetsky (1985) the human spine, the pelvis and the shoulder girdle can be described as behaving like a resonating pendulum system. In this system, the most energy efficient state of this system corresponds with the most "comfortable" walking speed. In humans this has been recorded to be the case at a walking speed of approximately 2.6 km/h. As in all locomotion modes, bipedalism is performed in the field of gravitation. The pendulum system can be seen as a mechanism which uses the field of gravitation to its advantage in order to increase the energy efficiency of the bipedal gait. The resonating pendulum is able to transform potential into kinetic energy. In human bipedalism, as stated above, the walking body performs a coupled rotation-

flexion motion; which resembles a figure 8. The spine is flexed both laterally and in the sagittal plane (see figure 1.8). The most "comfortable" walking speed is defined as the speed where the amount of torque that must be transmitted by the intervertebral joints can be generated by the trunk muscles alone. Above this critical speed, the torque requirement is such that additional power sources must be found. This is the role of the hip extensors.



A: Lateral bending of the spine B: Counter rotation of pelvis and shoulder

Figure 1.7 Components of the coupled rotation motion of the spine during walking. Adapted from Gracovetsky (1985), p. 209

With the coupled rotation-flexion motion, axial torque is produced, since it is impossible to bend a rod-like structure (in this case the spine) at the same time in two different directions without creating torsion in the structure (Badoux, 1974; Lovett, 1903). Figure 1.9 illustrates the three-dimensional interpretation of this coupled rotation motion. Gracovetsky (1986) found that this axial torsion is used to "drive" the pelvis and –ultimately – the lower limbs. At each step, the oscillation of the pelvis creates an alternating angular momentum that must be balanced. Synchronous opposite motion of the shoulders has indeed been observed; it creates an opposite angular momentum that exactly balances that of the pelvis. The sagittal flexion-extension motion moves the centre of gravity in a wave-like motion along the line of locomotion in humans. This is due to the extension movement of the legs as well as variation of the degree of lumbar lordosis.

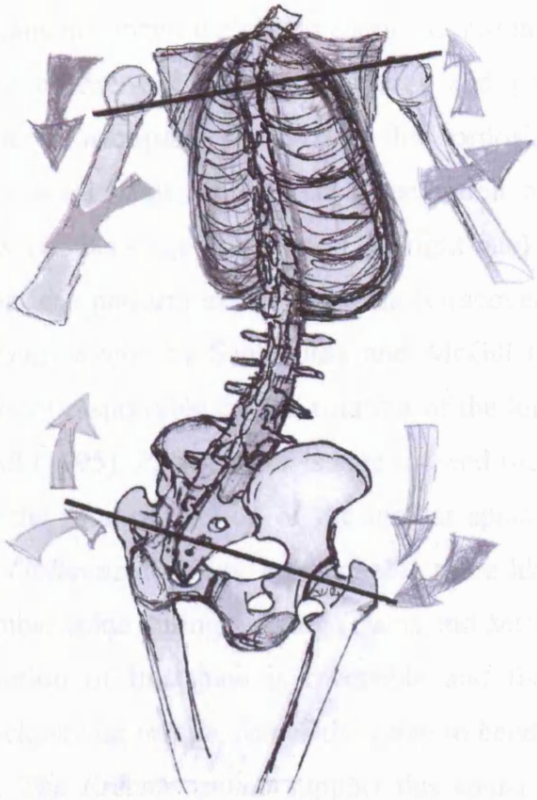


Figure 1.8 Three-dimensional interpretation of coupled rotation motion. Lines are drawn through the plane of the femoral heads and through the humeral heads

Human walking cycle

A walking cycle in bipedal locomotion can be broken down into three main events; these are heel-strike, mid-stance, and push off (also called toe off) (Trew and Everett, 1997) (see figure 1.10). In a walking cycle, starting with the left leg advancing, the right leg is in extension and contractions of the lateral flexors force the spine to flex to the left. Hence lateral flexion of the spine is induced. The left vertebral facets are strained and the spine flexes in the sagittal plane as it bends to the left. In contrast to forward bending, flexing the spine sagittally can be "translated" with reduction of the degree of the lumbar lordosis. This effect is most evident the moment the left heel strikes and the movement of the right hip extensors rotates the pelvis backwards. At right push off, the angular displacement of the pelvis is at its maximum. The pelvic rotation is controlled and achieved by the induced axial torque that arises from both, the lateral bend of the spine and its degree of lumbar lordosis. As the right foot leaves the ground, the spine must be counter-rotated to initiate the next cycle. This can be achieved by unwinding

the ligament apparatus of the spine. Axial torque is reduced due to the coupled motion of the spine when the ligaments uncoil the elastic energy stored in the wound up spine is being transferred to the counter-accelerating shoulders and pelvis. When the spine reverses its rotation, it is necessary to correct the lordosis, maintain the axial compression, and reduce shear. This requires an accentuation of the lumbar lordosis. For this, the *Psoas major* (at this stage of the cycle the right one) has been hypothesised to be the only muscle that can perform exactly this task (Gracovetsky, 1986). However, recent studies of the *Psoas major* by Santaguida and McGill (1995) reveal that the *Psoas major* is probably not responsible for the rotation of the lumbar spine. According to Santaguida and McGill (1995), *Psoas major* is able to bend the lumbar spine laterally but contributes little to the rotation motion of the lumbar spine. Thus, the abdominal wall muscles, especially *Obliquus externus,* are probably more likely candidates for the role of rotator of the lumbar spine during walking (Davis and Mirka, 2000; Mirka et al., 1997). The coupled motion of the spine is reversible and the *Psoas* induced and controlled axial counter-clockwise torque, forces the spine to bend to the right, the spine begins to straighten up. The *Erector spinae* support this spinal motion which is now repeated at each step as the spine resonates in the field of gravity.

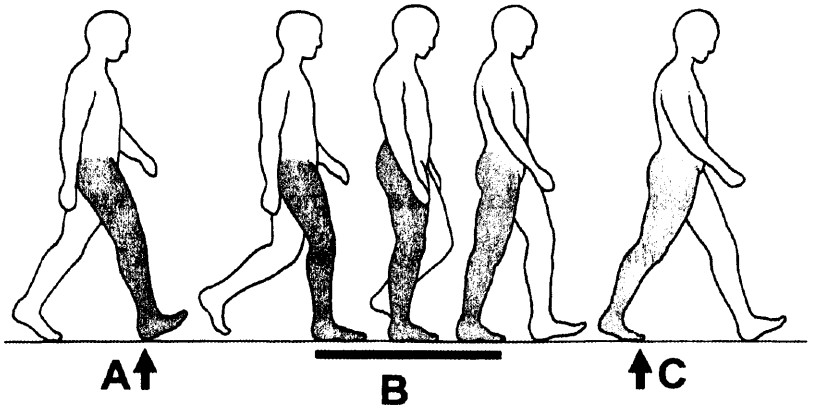


Figure 1.9 Human bipedal walking cycle: **(A)** heel strike, **(B)** mid-stance, and **(C)** push off. Adapted from Aiello and Dean (1990), p. 269

1.6.5 How to maximise energetic efficiency in human bipedal walking

Walking uses an "inverted pendulum" principle in which the centre of mass vaults over the extended leg during the mid stance phase (figure 1.11), effectively exchanging potential and kinetic energy out of phase with every step (Alexander, 1992). This oscillation motion of the trunk (as expressed in the flexion-extension motion of the

lumbar spine in previous section 1.6, p. 50.) enables the lumbar spine (its ligaments, the intervertebral discs, and the musculature) to store and release energy which generates a smooth and energy efficient walk. At low speed (approximately 2.6 km/h), the energy stored and released in the spine is supplied entirely by the trunk muscles, since walking at this speed only generates small pelvic oscillations.

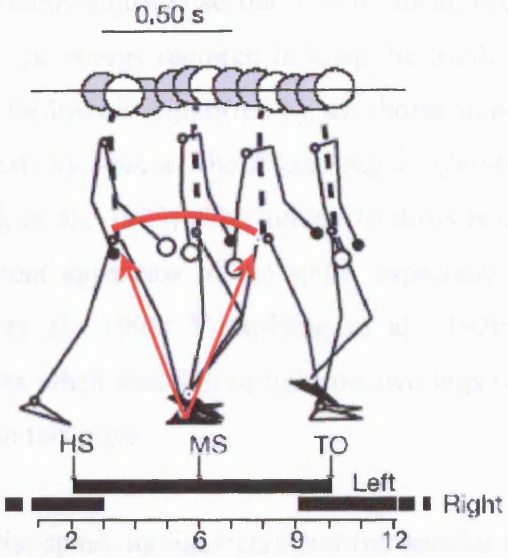


Figure 1.10 Inverted pendulum principles in bipedal walking: arc describes the motion of the trunk over the hip joints, radius consists of leg length. Note the head "bobbing" along with the motion of the trunk. HS = heel strike, MS = mid stance, TO = toe off. Adapted from Bramble and Lieberman, (2004), p. 346

A remarkable adaptation to resist torque forces is observed in the articular joints. It has been shown that their ability to transmit torsion forces is enhanced significantly when they are under compression load although this varies with the degree of flexion of the lumbar spine (Adams, 1985; El-Bohy, 1989). The ability to resist not only torque but also shear stress is further enhanced by the sagittal orientation of the zygapophyseal joint facets (Cihak et al., 1989). Hence, the body weight increases the ability of the joints to resist torque which stabilizes the erect position of the spine and adds to the amount of energy that can be stored and released by the lumbar spine. Also, the ability to resist relatively large torque allows for greater pelvic oscillation being exerted. This is important because with an increase of stride length, the pelvic oscillation (or rotation) is increasing too (Schmid and Piaget, 1994).

As discussed above, the degree of lumbar lordosis is linked with the amount of elastic energy that can be stored and released in the lumbar spine to initiate the walking cycles

(Gracovetsky, 1986). The more the lordosis is accentuated, the more potential energy is stored and the more can be released for the next cycle. Superimposed over this mechanism, the degree to which the spine as a whole is twisted, counteracts the rotation in the pelvis against the shoulder girdle and this helps to keep the walking cycle smooth and minimise expenditure of energy (Gracovetsky, 1986). With this motion, the upright position of the trunk is constantly adjusted so that it is balanced properly over the pelvis and the femoral heads, thus the energy required to keep the trunk upright is minimized. In this function, the lumbar lordosis is supported by the thoracolumbar fascia, trunk and back muscles, namely the *Erector spinae*, the *Psoas major*, *Quadratus lumborum*, and the hip extensors (Vleeming et al., 1995). The lumbar lordosis is maintained by gravity and supported by the ligament apparatus of the spine, especially the *Ligamenta flava* (Fasana, 1976; Olszewski et al., 1996; Yong-Hing et al., 1976). In comparison to modern humans, chimpanzees when standing upright on two legs require a considerable amount of energy to maintain this pose.

When torque is applied to the spine, its ligaments and the annular fibres of the *Annulus fibrosus* are stretched and as the motion is reversed, the tension in ligaments and in the *Annulus fibrosus* fibres is diminished. The fibres in the other layers of the *Annulus fibrosus* alternately extend and relax. The energy put into stretching the fibres of the intervertebral discs and ligaments of the spine represents the natural energy storage mechanism that becomes available as they recoil and energy is transferred between the spine and the limbs during locomotion. The torque forces transmitted during walking through a section of a body at L4 show that maximum torque strength is usually reached at heel strike. Gait studies have shown that in walking, the lateral bend of the spine is of the order of 7° for the entire spine. This small degree of lateral bend (in combination with the flexion extension motion of the spine) induces an axial torque that has the correct action of the pelvis during walking. Predictably, as the rate of walking is increased the amount of lateral bending is increased because a greater torque force is also required to increase the forward velocity. The basic ability to flex laterally coupled with true lordosis confers the capacity to generate sufficient torque to move the pelvis and lower extremities. Once the pelvis has been rotated, the legs do their own thing to follow pelvic motion.

1.6.6 Sexual dimorphism in human bipedal kinematics

Both sexes in *Homo sapiens* engage exclusively in habitual bipedal walking as the main locomotor mode. Nevertheless, there are important biomechanical differences observed in the bipedal gait of men and women. For example, Li et al. (1996) and Oberg et al. (1993, 1994) found differences between the sexes in gait parameters such as step length and gait speed but not in step frequency. Even more interesting, Schache et al. (2003) and Li et al. (1996) report significant differences in angular rotation of the lumbo-pelvic–hip complex during walking between men and women. These results highly likely relate to the well known sexual dimorphism in pelvic morphology which evolved due to obstetric necessities (Häusler and Schmid, 1995; Ruff, 1996; Schultz, 1949).

1.6.7 Differences between bipedal walking and running

The main differences between bipedal walking and running kinetics and kinematics are seen in that during bipedal walking, one foot always rests on the ground, whereas in running, there is a period where both feet are off the ground (Alexander, 1992). Contact with the ground in walking occurs through heel-strike, whereas in running this is replaced by a mid-foot strike (Bramble and Lieberman, 2004). The legs are kept fairly straight both during the time a foot contacts the ground (heel strike) as well as during mid-stance and push off in walking, whereas in running, legs are mostly bent at hip and knee joints. Most importantly, during running, the trunk is flexed whereas in walking, it is kept upright (see figure 1.12). The inverted pendulum principle of cyclically transforming potential and kinetic energy is not applicable to running, since due to the airborne period, the whole body rises and falls – not just the trunk. Thus, energy efficiency is achieved through by a "bouncing ball" principle, where the whole body acts as the "bouncing ball".

Although all bipedal gaits are inherently unsteady, running is more so than walking. To enhance trunk stabilization and torque counteraction in the trunk during running, humans probably developed the ability of isolated trunk rotation (Bramble and Lieberman, 2004; Carrier, 1984). In addition, humans are set apart from other hominoids in that there is relatively greater structural independence of the pectoral girdle and head. This is functionally advantageous for the independent counter-rotation of the pectoral girdles and arms necessary to counter-balance the legs in running and to minimize axial rotation of the head (Bramble and Lieberman, 2004; Carrier, 1984).

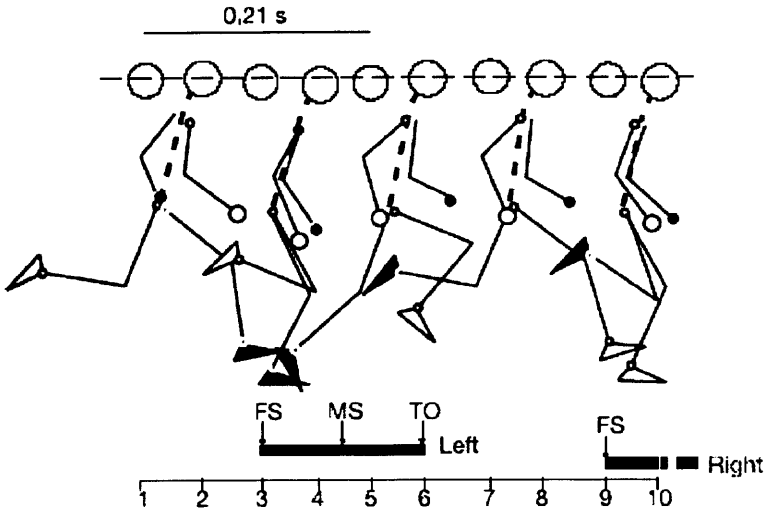


Figure 1.11 Human running cycles: Note forward leaning of the trunk, mid foot strike, and bent hip and knee joints during the whole cycle. In contrast to walking, the head does not follow the up and down motion of the trunk. FS = foot strike, MS = mid stance, TO = toe off. Adapted from Bramble and Lieberman (2004), p. 346

1.7 Locomotion in non-human hominoids

The role of the hominoid vertebral column differs somewhat from the one commonly ascribed to the mammalian spine in the previous section: during arboreal locomotion (climbing), great apes do not produce propulsion forces exclusively with their hindlimbs. Great ape locomotion is therefore described as forelimb dominated and it is the most so in *Hylobates* and *Pongo* and least in *Gorilla* (Ashton et al., 1965a; Ashton et al., 1965b; Jungers, 1983; Oxnard, 1983; Schultz, 1933). As will be seen later, this has considerable consequences for the trunk and vertebral column morphology of the great apes. One of these is strongly reduced spine mobility. In the following section, locomotor repertoires and the role of the lumbar spine in great ape taxa are introduced.

1.7.1 Locomotor repertoires of extant hominid taxa

Primates, although fundamentally quadrupeds like the majority of mammals, show considerable flexibility in locomotor behaviour; almost all taxa are versatile not only on the ground but also in arboreal surroundings (Schultz, 1969a). As most primate species live in highly diverse and three-dimensional habitats (trees), this strategy is very successful. Some of the more specialized locomotor modes which evolved in various primates include bipedal leaping and vertical clinging, quadrupedal walking-climbing,

hanging-climbing, brachiation, and bipedalism (Badoux, 1974; Hunt et al., 1996; Napier and Napier, 1967). Bipedalism is most developed in humans but has also been observed in other primate taxa (e.g. *Ateles, Hylobates, Pongo* and *Pan*) (Baldwin and Teleki, 1976; Doran, 1993a; Fleagle, 1976; Jenkins, 1990; Moynihan, 1976; Napier and Napier, 1967; Remis, 1998).

African great apes (*Gorilla gorilla* and *Pan troglodytes*)

African apes are typical primates in the diversity of their locomotor repertoire. They use different locomotor modes according to their immediate environment. The African great ape postcranium predominantly displays adaptations to arboreal locomotion, especially to vertical climbing and arm-hanging (Hunt, 1991b). The grasping hands and feet, long fore-limbs, and very mobile hip, ankle, elbow, and wrist joints are key features in their adaptation to hanging-climbing as well as suspensory behaviour (Fleagle, 1992; Hunt, 1991b; Keith, 1903; Napier and Napier, 1967; Richmond et al., 2001; Schultz, 1969b; Tuttle and Basmajian, 1974). However, recently the question has been raised as to whether or not great ape postcranial adaptations are better seen in relation to greater safety using arboreal substrates than in relation to locomotor energetic efficiency (Pontzer and Wrangham, 2004). The authors suggest that climbing safety might be the most likely selective pressure shaping great ape anatomy (rather than energy efficiency in locomotion, although this is difficult to assess to date, due to lack of energy consumption during locomotion data for all great apes). Arboreal locomotion of African great apes consists of vertical climbing, scrambling, and to no small degree of quadrupedal walking on larger branches. To enter a tree, African great apes usually prefer to proceed on sloping substrates instead of vertically climbing up tree trunks (Hunt, 1991b).

The African ape locomotor repertoire includes large amounts of terrestrial locomotion. In this, both African apes frequently engage in a locomotor mode called knuckle-walking. In knuckle-walking, the forelimbs are mainly engaged in body weight support and the hindlimbs act as the generators of forward motion. Knuckle-walking involves adaptations in the forearm, carpals, metacarpals and proximal phalanges since they bear the most weight and resist the largest forces during locomotion (Richmond et al., 2001; Tuttle and Basmajian, 1974). Knuckle-walking is used at various speeds (slow to fast) by both taxa. Besides knuckle-walking, short periods of bipedalism have been reported for both African ape taxa (Doran, 1993b; Doran, 1997; Remis, 1995). However, the

form of bipedalism used by African apes differs from the one seen in modern humans. They usually do not extend their legs fully in bipedal gait as seen in modern humans and there is no combined flexion-rotation motion observed in the lumbar spine (Jenkins, 1972).

Asian great apes *(Pongo pygmaeus)*

Among the great apes, *Pongo* is the most arboreal taxon. It is also the largest canopy living mammal (MacKinnon, 1974). *Pongo* has a varied arboreal locomotor repertoire - the most common locomotor modes displayed are clambering (brachiation with additional securing of position with the feet), brachiation, tree-swinging, vertical climbing, and some quadrupedal walking on arboreal substrates (Cant, 1987a; Cant, 1987b; Hunt, 1991b; Isler and Thorpe, 2003; MacKinnon, 1974; Thorpe and Crompton, 2005). In contrast to the fast travelling and predominantly truly brachiating and jumping small bodied gibbons (the other Asian ape family), *Pongo* moves slowly through the canopy. Occurrence of jumping is very rarely observed and if so in the context of flight in great distress (MacKinnon, 1974).

Orang-utans rarely come down to the ground and do not engage in terrestrial locomotion frequently. However, if this is the case, the term "fist-walker" (Tuttle and Basmajian, 1974) has been coined to describe their quadrupedal gait, since they hardly ever walk on their knuckles. Quadrupedal as well as supported bipedal walking has been observed on arboreal substrates in which case the substrate is usually firmly griped (Cant, 1987b; MacKinnon, 1974).

1.7.2 Differences in locomotor repertoires between extant great apes

Differences between African and Asian apes

The African great ape locomotor repertoires are different from the ones observed in Asian great apes. Asian apes engage more frequently in brachiation, hand over hand climbing, hand-foot hanging, and clambering (Cant, 1987b; MacKinnon, 1974). Conversely, African apes engage more frequently in arm hanging and vertical climbing (Hunt, 1991b). In general, *Pongo* relies predominantly on forelimb propulsion in arboreal locomotion and uses hindlimbs to secure its position in the arboreal substrate (Schultz, 1953). Orang-utans seldom walk quadrupedally on arboreal substrates whereas

African apes are more often observed to do so (Hunt, 1991b). Asian apes also climb with longer stride frequencies and considerably more motion in the limb joints (Isler, 2005). This in accordance with the observations that *Pongo* hip abductor muscles (compared to African apes) are more powerful – with the consequence that their hip joints can be moved with more power and mobility (Sigmon, 1974). In the canopy, orang-utans move more slowly than African great apes. On the ground, no gallop sequences have been recorded for *Pongo*, whereas for African apes, they are more common (MacKinnon, 1974).

Differences between African apes

Since *Gorilla* and *Pan* differ considerably in body size, inter-specific differences in locomotor repertoires might be expected. Doran (1997) investigated the development of the *Gorilla* and *Pan* locomotor repertoires throughout ontogeny. She reports that compared to chimpanzees, *Gorilla* locomotor development is greatly accelerated so that much of the inter-specific locomotor variation between age-groups can be explained by body size (Doran, 1997). Thus, when chimpanzees and gorillas are of similar sizes (although widely disparate in age), they perform very similar locomotor activities. Nevertheless, gorillas never show as high an incidence of suspensory behaviour as chimpanzees during ontogeny. In general, differences in locomotor repertoires between *Gorilla gorilla* and *Pan troglodytes* consist predominantly of differences in frequencies of common locomotor modes. Thus, climbing "techniques (e.g. vertical climbing) used by *Gorilla gorilla* and *Pan troglodytes* are very similar to each other (Isler, 2003), but the frequency of arboreal climbing (and vertical climbing for that matter) is not; gorillas spend less time in trees than *Pan troglodytes* (or *Pan paniscus*) (Doran, 1993b; Hunt, 1991b).

Differences between great ape sub-species

Between sub-species too, differences in the locomotor repertoire have been reported. Mountain gorillas (*G. g. beringei*) seem to spend considerably less time in trees (and thus are less engaged in arboreal locomotion) than the lowland sub-species (*G. g. gorilla* and *G. g. graueri*) (Taylor, 1997). The locomotor repertoire of bonobos (*Pan paniscus*) contains more arboreal locomotion than that of *Pan troglodytes* (Isler, 2003). Doran and Hunt (1994) showed that considerable differences in the habitat of different populations of each species had a smaller impact on the locomotor repertoire than the inter-specific differences observed. It has been observed that on Borneo, male and

female orang-utans engage in equal amounts of tree-swaying whereas on Sumatra, males engage in this locomotor mode far more often than do females. On Borneo, males sometimes travel on the ground between trees whereas females rarely leave the canopy and lower levels of tree branches (Cant, 1987b). On Sumatra on the other hand, both taxa hardly ever come to the ground, probably due to larger predator pressure caused by the presence of Sumatran tigers (Cant, 1987b).

Sexual dimorphism

It has been postulated that sexual dimorphism in body size and weight not only has an influence on the locomotor repertoire but also the kinematics and biomechanics of the locomotor modes. Therefore, in *Gorilla* which is highly dimorphic in body size, sexual dimorphism in locomotor repertoire as well as locomotor modes might be expected and these differences could be expressed as differences in the postcranial morphology of males and females. Remis (1995, 1999) reports that male gorillas, when compared to females, climb trees less frequently and if they do climb, they stay closer to the core and do not forage too far into the tree periphery. The same is observed for chimpanzees. Both *Pan paniscus* and *Pan troglodytes* females spend considerably more time in the trees than the males. In contrast to *Gorilla*, both *Pan* species are far less sexually size dimorphic, hence other factors such as domination of the easily accessible food sources on the ground by males could influence the amount of climbing in the locomotor repertoire (Remis, 1999). Intra-specifically, it has been reported that male *Pongo* use larger substrates, closer to the core of trees than females and that they use more supported positions (sitting, bipedal standing, tripedal standing) than females, which are more often engaged in suspended postures (hand-foot hanging, one hand hanging) (Cant, 1987a). Recent studies also show that parous females move more "cautiously" through the canopy than do females without offspring (Thorpe and Crompton, 2005). In Borneo, male Orang utans are observed more often on the ground than females (MacKinnon, 1974).

To summarize the differences in locomotor repertoire within and between great ape taxa, it can be said that Asian apes are far more versatile in arboreal locomotion and rely heavily on this form of locomotion. Therefore, they are the most arboreal recent taxa in this study. Of the African ape taxa in this study, *Pan troglodytes* is the more arboreal one, whereas *Gorilla* is more often on the ground but uses arboreal substrates on a

regular basis. Compared to all great ape taxa, modern humans have the least versatile locomotor repertoire: it consists exclusively of bipedal walking and running.

Intra-specific differences between age groups

The locomotor repertoires of both, *Gorilla* and *Pan* change during postnatal ontogeny. Whereas *Pan* and *Gorilla* individuals cling to their mothers during the first phase of infancy (first year of life), juvenile gorillas as well as chimpanzees show higher frequencies of arboreal locomotion than adults (Doran, 1993b; Isler, 2005; Pontzer and Wrangham, 2004). Sub-adult African apes climb with higher stride frequencies and higher limb excursion than adults (Isler, 2005). At the same time, adult gaits are energetically more efficient than those of juveniles (Pontzer and Wrangham, 2004).

Studies investigating differences in locomotor repertoire between sub-adult and adult orang-utans are very scarce. The few studies that exist indicate that in *Pongo*, both sub-adult and adult individuals spend equal time in the forest canopy. When compared to adults, MacKinnon (1974) observed higher frequencies of brachiation and vertical climbing in juvenile orang-utans. According to Isler (2005), juvenile *Pongo* specimens climb vertically more frequently than adult specimens and with a higher limb cycle frequency which also was more symmetric than in adults (Isler and Thorpe, 2003). In general, juveniles show a reduced range in joint motion. These intra-specific differences in vertical climbing locomotion between sub-adult and adult individuals are seen in relation to differences in body size and weight between the adults and sub-adults (Isler, 2005).

1.7.3 The great ape vertebral column in locomotion

As mentioned previously, great ape taxa differ from other mammals in that their propulsive forces during locomotion are not exclusively produced by the hindlimbs. This alters the role of the lumbar spine – particularly in arboreal locomotion but considerably in great apes. Thus, in the following sections, the role of the lumbar spine in the locomotion of great apes is discussed. Pontzer and Wrangham (2004) and other workers (Ashton et al., 1971; Ashton and Oxnard, 1975; Keith, 1903; Schultz, 1933; Schultz, 1938; Slijper, 1946) agree that the great ape postcranium shows extensive adaptations to arboreal locomotion. Therefore, the considerable amount of terrestrial locomotion seen in African great apes is interpreted as a secondary development and

adaptations to it are less extensive than those to arboreal locomotion. Nevertheless, since terrestrial locomotion is crucial in the locomotor repertoires of African apes, in the subsequent discussion the adaptations in the trunk of the living apes to locomotion are divided into those for arboreal locomotion and those for terrestrial locomotion.

During arboreal locomotion -especially hanging-climbing and scrambling - the great ape lumbar spine is subjected to reduced amounts of compressive forces due to the preference of forelimb use (Oxnard, 1983). This is considered a major difference in loading pattern between humans and great apes as well as between great apes and terrestrial mammals.

Arboreal locomotion

The great apes of Africa and Asia are the largest extant tree living animals. In general, tree living animals are much smaller, and thus support of animal of the size of a great ape on small substrates such as tree branches requires special adaptations. Great apes differ from smaller climbing primates in that they often hang safely under branches rather than trying to balance their considerable weight on top of the substrate. Except for the gibbons, which do a considerable amount of leaping and swinging from branches, the African apes as well as Orang utans are "quadrumanous" climbers and they leap rarely from one tree or branch to another. However, some quadrupedal walking on a tree substrate has been observed in all great apes (Cant, 1987b; Doran, 1993b; MacKinnon, 1974; Napier and Napier, 1967; Remis, 1998).

Besides these behavioural adaptations, the great ape postcranial morphology reflects extensive adaptations to arboreal locomotion. These consist of highly mobile shoulder and hip joints, which show little restriction in any particular direction (Sonntag, 1924). Of all the great ape taxa, orang-utans seem to have the most mobile hip and shoulder joints (Ashton and Oxnard, 1964; Schultz, 1969a; Sigmon, 1974). Extensive suspensory behaviour and the lifting of heavy body weight up a tree require a considerable amount of muscle power. The main muscles for climbing in apes seem to be *Trapezius* and *Latissimus dorsi*. The *Trapezius* of *Gorilla* and *Pan* has an extended occipital origin which laterally connects with the insertion of the *Sternocleidomastoideus* (Sonntag, 1924). Often, its inferior insertion is fused with the *Latissimus dorsi* and the outer border reaches the *Acromion* and surpasses the whole length of the scapular spine (Slijper, 1946; Sonntag, 1924; Swindler and Wood, 1982). The *Latissimus dorsi*

originates from the *Fascia thoracolumbalis*, as well as from the iliac crests. It has a tendency to fuse with the *Teres major* and its insertion in the bicipital groove of the humerus seems to be distinctively ribbon-like (Sonntag, 1924).

Large muscles like those involved in climbing in great apes need stable points of origin to exert their full power. Therefore, in contrast to the hyper-mobile limb joints (shoulder, hips, ankle, etc) mobility in the great ape trunk is generally small. This minimizes torsion and bending forces acting on the great ape trunk (Hunt, 1991b; Ward, 1993b). The reduced mobility of the great ape trunk (in comparison to *Homo sapiens* and all other non-hominoid primates) results from all great apes having a very short lumbar spine which brings the thorax and the pelvis closely together. Simultaneously, the iliac blades of the great ape pelvis are dorsally elongated and in the case of some male gorillas almost touch the last pair of ribs (Schultz, 1961).

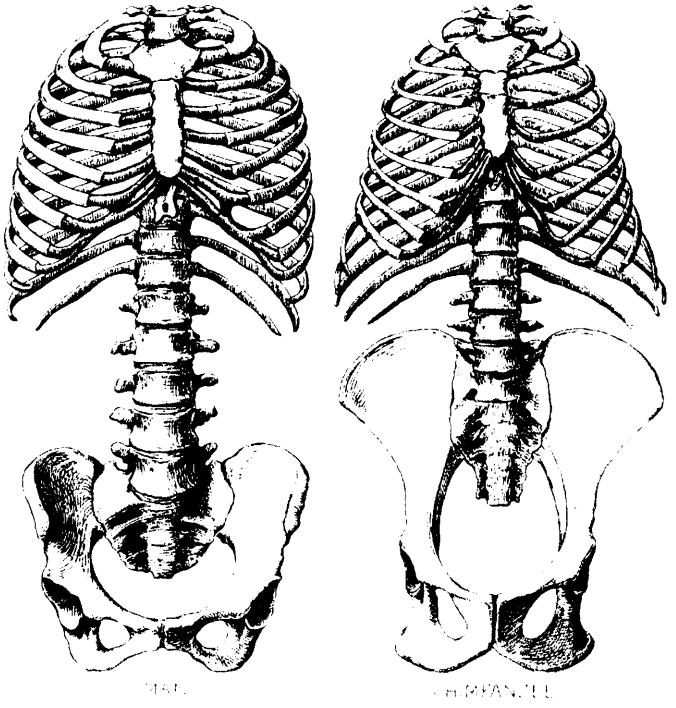


Figure 1.12 Proportions of lumbar spine capable of free motion in humans and chimpanzees. Note how in *Pan* (as well as in other great apes) the last pair of ribs is in close vicinity to the iliac crest. *Homo sapiens* and *Pan* are scaled to comparative size. Adapted from Schultz (1950b), p. 41

These differences in great ape trunk morphology compared to that of modern humans are illustrated in figure 1.13 which shows clearly that in the great ape lumbar spine, lateral bending mobility is greatly reduced because the elongated iliac blades act as

"splints" for the lumbar spine (Schultz, 1969a; Sonntag, 1924). Trunk stability during arboreal locomotion in all great apes has been regarded as a main factor for closely resembling trunk (thorax and pelvis) morphology between all great ape taxa (Hunt, 1991a; Schultz, 1933; Schultz, 1938).

The distinctive trunk morphology implies that great apes lack the ability to produce large propulsion forces due to sagittal flexion-extension motion of their lumbar spine (as do most land living mammals, including humans). Great apes highly likely compensate for the lack of propulsion production in the lumbar spine with the greater range of motion in their shoulder and hip joints (Isler, 2005; Thorpe et al., 1999), thus pulling themselves up along the arboreal substrate.

Terrestrial locomotion

The forces the great ape lumbar spine is exposed to during terrestrial locomotion are not particularly different from those of other mammals (Slijper, 1946). The lumbar spine therefore predominantly resists bending forces in the coronal plane and resists compression loads caused by body weight (Davis, 1961; Gracovetsky, 1986; Slijper, 1946). During terrestrial locomotion in African apes, the forelimbs and shoulder girdle support part of the body weight, which reduces the compressive loads transmitted through the lumbar spine (Badoux, 1974; Slijper, 1946).

In terrestrial locomotion, the hyper-mobile joints of great apes can compensate to a degree for the lack of motion (flexion-extension) in the lumbar spine, which is producing propulsive forces in most land-living mammals. Nevertheless, with regards to energy efficiency, great ape (chimpanzee) terrestrial locomotion has been estimated to be relatively costly when costs were represented by amount of oxygen consumption during locomotion (Taylor and Rowntree, 1973) and compared to other quadruped mammals of similar size (Li et al., 1996; Nakatsukasa et al., 2004; Pontzer and Wrangham, 2004; Sellers et al., 2003). Both species are usually not seen engaging in long distance travelling at higher speed or at long distance travelling at all (Bramble and Lieberman, 2004; Carrier, 1984; Jenkins, 1972).

1.7.4 Comparison of human and chimpanzee bipedal walking gaits

The bipedal walking gait of chimpanzees has been described as "lurching" and lacks the effortlessness of the modern human (Jenkins, 1972; Li et al., 1996; Tardieu et al., 1993). In bipedal gait, the chimpanzee pelvis undergoes a reorientation (due to upright posture) but the pattern of femoral flexion and extension remains the same as during quadrupedal locomotion (Jenkins, 1972). Even more importantly, according to Tardieu and co-workers (1993), the main difference in the bipedal gait of humans and chimpanzees lies with the synchronization of the transverse and vertical displacement of the pelvis during locomotion. Human bipedalism is distinguished by the high degree of synchronization of these two movements. In chimpanzees, on the other hand, the vertical and lateral displacements of the pelvis are not associated with any pattern of periodic synchronization. Tardieu et al. (1993) suggest that the chimpanzee's bipedal gait resembles the gait of a tightrope-walker; the centre of mass hardly oscillates but its small divergence from the median line of walking is achieved at the expense of large and asymmetric movements of dynamic adjustments, and hence the lack of periodical patterns. Although the study by Tardieu et al. (1993) shows the differences in human and chimpanzee bipedal walking, it does not explain why human bipedalism requires synchronization of the sagittal flexion-extension motion with the lateral bending one. However, we have seen earlier in the chapter why this synchronization is important for the energetic efficiency of the human bipedal gait (Gracovetsky, 1985; Gracovetsky, 1986).

1.8 Fossil hominin locomotion

1.8.1 The discovery of the first australopithecine fossils and their role in human evolution

Ever since Dart discovered the first australopithecine fossil, its interpretation, its taxon affinities and how subsequently found fossil hominins are positioned in relation to it, has changed a great deal over the last few decades. The fossil described by Dart consisted of a partial infant skull and brain endocast. Its age was estimated to be two to three years, based on human life history. The fossil was discovered in a limestone cave in Taung, South Africa. The original site has now been destroyed and there is considerable doubt about the fossil's geological age; recent studies of uranium isotopes and fauna comparisons indicate time ranges from as young as 1.0 to 1.2 myr (Partridge

et al., 1991) and as old as 2.6 to 2.8 myr (Tobias et al., 1993). Dart named the fossil *Australopithecus* (southern ape) *africanus* instead of *Homo*, arguing that the size of its brain and brain case were rather small (Dart, 1925). On the other hand, he noted that its teeth were more similar to *Homo* than to the apes and that the position of the *Foramen magnum* on the base of the skull clearly indicated that *Australopithecus africanus* balanced its head on a permanently erect vertebral column. This made it a crucial find because it pointed out that the evolution of bipedalism in the hominin lineage appeared early and clearly before any encephalization had taken place. However, the interpretation of *Australopithecus africanus* as a hominid capable of human-like upright walking based solely on evidence gathered from the Taung specimen, Sts5 (Ms. Ples), and Sts14 (partial postcranium, see later for more details) has subsequently been challenged by (Ashton, 1957; Ashton and Flinn, 1975; Oxnard, 1975; Zuckerman et al., 1973). They demonstrated that throughout postnatal development, in African great apes the position of the *Foramen magnum* and the occipital condyles change from a more human-like position to the adult ape position. It could therefore not be ruled out that - had the juvenile Taung specimen reached maturity - the position of its *Foramen magnum* would have been considerably more ape-like. Furthermore, the position of the occipital condyles is not exclusively influenced by trunk posture. Biegert and Maurer (1972) claim that with regards to the position of the occipital condyles, brain size should be taken into consideration. In summary, from an isolated skull, and a juvenile specimen, it seemed difficult to interpret the locomotor repertoire of the australopithecines.

It is worth noting that throughout the first half of the 20th Century, australopithecine fossils were not recognized as potential human ancestors; they are hardly mentioned in this context because of the prevalence of the view that the human ancestor evolved a large brain before habitual bipedalism e.g. Woodward (1925). This view was further supported by the discovery of the Piltdown Man (so called *Eoanthropus dawsoni*). With its relative great geological age and large brain case, it seemed to represent a perfect example of the *"encephalization before bipedalism"* evolution hypothesis towards modern man (which was favoured at the time). On a different level, this fossil also was preferred to represent an early human ancestor over the australopithecines because it suggested a European origin of modern *Homo sapiens*. Contemporary views and opinions apparently found African origins of modern humans difficult to accept.

Piltdown man turned out to be one of the worst hoaxes of science history. Skull fragments and a canine from a modern human cranium and the remnants of an orang-utan mandible were skilfully prepared and deliberately placed in some English Pliocene or early Pleistocene deposits, where they were subsequently found between 1908 and 1915 (Dawson and Woodward, 1913). It was only when the skull was exposed as a forgery in the 1950s (Oakley, 1949; Oakley and Hoskins, 1950; Washburn, 1953; Weiner, 1955) that other approaches to human evolution, such as today's now commonly accepted "*bipedalism before encephalization*" hypothesis could be explored further. With the Piltdown Man no longer swaying opinions in a misleading direction, the Taung skull as well as further *A. africanus* fossils (e.g. the skull Sts 5, Mrs. Ples and postcranial elements) found by Robert Broom at Sterkfontein and close by locations could finally be interpreted in a more satisfactory way (Broom, 1938a; Broom, 1938b; Broom and Robinson, 1947; Broom et al., 1950). These fossils turned out to be crucial in establishing the Australopithecines as potentially belonging to the lineage leading to modern humans as well as shedding more light on their adaptations to bipedal gait. Ironically, the current consensus holds that neither *Australopithecus africanus* nor the robust types (*Paranthropus*) of South Africa are to be placed in direct line leading to modern humans (McHenry and Berger, 1998; Wood and Richmond, 2000).

1.8.2 The issue of bipedalism in the fossil hominin record

In the case of fossil locomotor repertoires which differ from any seen in modern species a reconstruction is difficult since this reconstruction cannot be compared with the locomotor repertoires of living taxa. This difficulty in assessing fossil locomotor repertoires is expressed in the long standing debate of what the australopithecine locomotor repertoire consisted. Briefly, opinions varied from addressing australopithecines as habitual bipeds similar to modern humans to almost entirely arboreal creatures. The commonest held view is that the australopithecine locomotor repertoire is partially bipedal and partially arboreal. These two locomotor modes are combined in a way exclusive to australopithecines and not observed in any of the modern hominoid taxa. In the following sections, current views are introduced on the potential locomotor repertoires of australopithecine taxa and the biomechanics of australopithecine bipedal gait and arboreal locomotion.

Australopithecus africanus

Although the relations between *Australopithecus africanus* and modern humans are probably not resolvable, australopithecines nevertheless provide important clues to the adaptations to bipedalism associated with the origin of the human lineage and its divergence from that leading to living apes. The discovery of a partial skeleton of *Australopithecus africanus* (Sts14) in Sterkfontein, South Africa by Broom provides the best evidence so far that *A. africanus* was a habitual biped. The skeleton consists of a tibial fragment, a left femoral fragment, some fragments of the left and right hip bones, a partial vertebral column including a sacral fragment, some ribs and a few cranial fragments. Before the discovery of Sts14, various opinions about the locomotor habits of *A. africanus* prevailed. The *A. africanus* fossil material was not immediately considered to resemble humans more closely than apes. There were various opinions about the affinity of the material - among these it was thought that the femoral fragment resembles *Gorilla* most closely (Schwartz, 1936). However, based on examinations of the lumbar spine, the sacrum and the pelvis, as well as the femur and tibia, Robinson (1972) concluded that the *A. africanus* material belonged to a species which

"*...was habitually erect bipedal and had a sacrum that resembled closely that of modern man in both anatomy and orientation. Therefore the spinal column must have been functioning in the position and in the manner characteristic of man*" (Robinson, 1972), p. 108

In summary, it was thought that *Australopithecus africanus*, despite having a rather wide pelvis, had a locomotor repertoire not distinguishable from modern humans and that the biomechanics of its bipedal gait were not at all that different from *Homo sapiens*. This opinion was widespread until the mid 1970's and early 1980's. Doubts on this interpretation of the australopithecine postcranial morphology, in particular the pelvis, voiced in 1973 by Zuckerman et al. (1973), were soon followed by similar studies by McHenry and Corruccini (1975) which produced similar results. Nonetheless, general opinion prevailed that *A. africanus* was a habitual biped in the style of modern humans.

Australopithecus afarensis

The discovery of a new, Eastern African australopithecine taxon in the 1970s shed further light on the evolution of bipedalism in the hominin lineage. The fossil remains

attributed to this taxon are older than the ones recovered for *A. africanus* and come from sediments that have been relatively reliably dated between 3.4 and 3 myr. In 1975 a partial skeleton more complete than any found before was recovered at the Hadar Location, Ethiopia (Johanson et al., 1982a). It is from this specimen, AL 288 (better known as Lucy), that most knowledge about the *A. afarensis* postcranium has been gathered. At first, based on a reconstruction of the pelvis (Lovejoy, 1979) and comparisons of the femur and tibia of Lucy with modern humans, it was considered that *A. afarensis* was a fully bipedal hominin, not different in its locomotor repertoire from modern *Homo sapiens*. The discovery of tracks of footprints in Laetoli, Tanzania dating approximately to 3.4 my (Drake and Curtis, 1987), corroborated the view that *A. afarensis*, to whom the prints were attributed, was a fully erect biped (Robbins, 1987; Tuttle, 1981; Tuttle, 1987). The footprints have been attributed to *A. afarensis* because fossil remnants of this taxon had been discovered in Laetoli (White, 1980; White and Suwa, 1987).

Although the tenet that bipedalism played an important role in the Australopithecine locomotor repertoire was not generally challenged (Ashton, 1957; Ashton and Flinn, 1975; Ashton and Zuckerman, 1956a; Ashton and Zuckerman, 1956b; Oxnard, 1975; Zuckerman et al., 1973), further studies of the postcranium of *Australopithecus afarensis* as well as *A. africanus* started to yield results which contradicted the view of australopithecines walking and running like modern humans. The initial description of the fossil was followed by a first wave of research projects which concentrated on differences in body proportions between modern humans and australopithecines and on the importance of the functional anatomy of the upper limb of Lucy (Schmid, 1983; Schmid, 1991; Senut and Tardieu, 1985; Stern and Susman, 1983; Stern et al., 1984). The latter turned out to be rather ape-like: the arms of *A. afarensis* are relatively long when compared to modern humans (Häusler and McHenry, 2004; Jungers, 1983; Jungers, 1988; McHenry, 1991b; McHenry and Berger, 1998; Schmid, 1983). The *A. afarensis* elbow joint resembles that of great apes more than that of modern humans (Bacon, 2000; Lague and Jungers, 1996). Further, the glenoid fossa of the *Scapula* is cranially orientated as is the case in great apes and not horizontally as in modern humans (Inouye and Shea, 1997; Schmid, 1983; Stern et al., 1984).

The footprints from Laetoli also where re-examined and further analysis indicated that – although they are more similar to prints left by modern humans than by chimpanzees –

they show some remarkable differences in how weight was transmitted from heel-strike to toe-off. These findings indicate that the pattern of weight transmission through the Australopithecine foot was not entirely congruent with the respective pattern in modern humans (Day, 1991; Schmid, 2000).

Thus, the ensuing debate soon centred not on the possibility that *A. afarensis* was using arboreal locomotion but also on the extent to which this played a role in the locomotor repertoire of *A. afarensis*. In the wake of this discussion, the biomechanics of australopithecine bipedalism were questioned as it was thought unlikely that adaptations to arboreal locomotion were compatible with a human-like bipedal gait and the ongoing investigation of the *A. afarensis*, as well as the re-examination of the *A. africanus* postcranial material seems to support this view. In recent years, a consensus has emerged that *A. afarensis* spent a considerable amount of its time in trees, yet when on the ground its predominant locomotor mode was a bipedal gait. However the commonly agreed consensus holds that the australopithecine bipedal gait was biomechanically different from that of modern humans as well as that of chimpanzees. For an excellent review of the topic see Stern (2000).

Since the discovery of *Australopithecus afarensis*, various other Australopithecine fossils have been discovered. Most important are the discovery of *Australopithecus anamensis* (Kanapoi and Allia Bay, estimated to be approximately 4 my years old) (Leakey et al., 1998); *Australopithecus ghari* (Bouri, Middle Awash, Ethiopia, estimated to be approximately 2.5 my years old) (Asfaw et al., 1999); and *Australopithecus bahrelghazali* (Koro Toro region, Chad, estimated to be approximately 4 my years old) (Brunet et al., 1996). Further, new fossils belonging to *A. ramidus*, from a site called Aramis, Ethiopia are estimated to be approximately 4.5 my years old (White et al., 1994), and shed new light on the potential root of the evolution leading towards *Homo*. Although a vivid discussion about the phylogenetic position of each fossil taxon is going on, this is only of peripheral interest to this study, since only the australopithecine taxa *A. africanus* and *A. afarensis* were included. The same is to be said for the early *Homo* taxa.

Homo erectus/Homo ergaster

The first *Homo erectus* fossils were excavated in Java and described by their discoverer Eugene Dubois (1894). This first discovery consisted of a tooth, the roof of a skull and a

femur, which were all excavated over a period of 11 months. Based on the accompanying fauna and the sedimentation of the location, Dubois dated the remains to the younger Pliocene. The biggest differences Dubois noted when comparing modern humans with the fossils were the shape and morphology of the skull. The postcranial elements were considered to be extremely robust when compared to modern humans, but there is no difference in shape or morphology (Dubois, 1894).

Since this first discovery, various Asian *Homo erectus* remains have been discovered in Asia as well as Near East. The African *Homo erectus* findings are now collectively addressed as *Homo ergaster* (see later in this section) (Wood and Richmond, 2000). Asian *Homo erectus* fossils span the large time period of 1.8 my to 50 kyr (Swisher et al., 1994; Swisher et al., 1996). This theoretically makes the Asian representatives contemporary to modern *Homo sapiens* (Swisher et al., 1996). In this context, the discovery of *Homo floresiensis* is of interest. If this particular discovery turns out to be the representative of an isolated *Homo erectus* population, then it would show that *Homo erectus* had a large intra-species variation similar to that of modern humans (Brown et al., 2004). The *Homo erectus* findings from Africa (Day, 1971; Leakey et al., 1964; Leakey and Walker, 1985) suggest that these remains are older than the Asian discoveries. Therefore, African *Homo erectus* fossils are referred to as *Homo ergaster*, underlining their older age and the lack of some distinctive cranial features only seen in the somewhat younger Asian *Homo erectus* fossils (Bräuer and Mbua, 1992; Bräuer and Rimbach, 1990). This is based on analyses of the mandibular premolar dentition. Also, *Homo ergaster* seems to be less specialised in cranial vault and base morphology than *Homo erectus*. *Homo ergaster* is represented in the present study by the Nariokotome specimen only. There is no risk of confusing the single African *Homo ergaster* specimen with those from Asia.

Modern *Homo sapiens* and *Homo ergaster*, as previous mentioned, resemble each other closely in postcranial morphology (Latimer and Ward, 1993; MacLarnon, 1993). That this is highly likely the case for overall body proportions as well became evident when in 1988, Brown and colleagues discovered the partial skeleton of a juvenile *Homo ergaster* specimen at the Nariokotome Location, near Lake Turkana, Kenya (Brown et al., 1985; Walker and Leakey, 1993). To date, this skeleton is the most complete fossil specimen of any extinct hominin (Leakey and Walker, 1993). Its body proportions do not differ from those of modern humans: the legs are relatively long, the arms relatively

short, the pelvis is typically modern human shaped and the thorax is barrel-shaped as seen in modern humans (Jellema et al., 1993). There is no doubt that *Homo ergaster* was a skilful biped, capable of covering long distances and he was also a good runner (Bramble and Lieberman, 2004; Ruff and Walker, 1993; Wang et al., 2004).

It is generally believed that *Homo ergaster/erectus* is the first large-bodied hominin taxon with a body shape closer to that of modern humans than to the australopithecines. *Homo ergaster/erectus* lacks the adaptations to arboreal locomotion still observed in australopithecines.

1.8.3 The fossil hominin spine in locomotion

The function of the spine of fossil hominins is in general not very different from the ones in recent hominin taxa. However, it is uncertain if the lumbar spine of australopithecines was as mobile as that of modern humans. It is probably safe to say that there are traits in the lumbar spine of the australopithecines that point towards it being more mobile than the great ape lumbar spine and it probably had a lumbar lordosis (Martelli, 1999; Robinson, 1972; Sanders, 1994). In the case of *Homo ergaster*, the assumption is that the lumbar spine was not much different from the one of modern humans holds; it possesses a relatively long and mobile lumbar spine with a functional lumbar lordosis.

Bipedalism

Stern and Susman (1983) suggest that Lucy's skeleton (*A. afarensis*) represents a mosaic of features. Some resemble great apes – such as the grasping toes, long arms, cranially orientated glenoid fossa, and the funnel-shaped thorax. These features presumably reflect adaptations to forelimb powered arboreal locomotion. Other features, such as the permanently adducted posture of the knees are distinctly human, whereas others such as pelvic morphology and tarsal bone arrangement are uniquely australopithecine. What does the mosaic postcranial morphology of mean in relation to australopithecine bipedalism?

Based on biomechanical investigations of the hip and thigh of *Homo* and *Australopithecus*, Berge (1994) suggests that australopithecine bipedalism probably had greater energetic costs than does the bipedalism observed in modern *Homo*. This is

because of shorter stride length and higher frequency estimated for *Australopithecus*. At the same time, the arrangement of the hip adductor in combination with the unique pelvic morphology of *Australopithecus* probably allowed for a favourable lateral hip and pelvis stabilization during walking (Berge, 1994; Häusler and Schmid, 1995; Schmid, 1983).

The australopithecine pelvis is different from that of the great apes and resembles that of modern humans most- but it shows several features which are exclusively australopithecine (Berge, 1984; Häusler, 2002; Häusler and Schmid, 1995; McHenry and Corruccini, 1975; Schmid, 1983; Stern and Susman, 1983; Zuckerman et al., 1973). These unique features are the expression of differences in biomechanics of the bipedal gait of australopithecines and modern humans.

The australopithecine femur and knee joint seem to resemble those of modern humans closely. This is in particular due to the presence of a bicondylar angle in the femur of australopithecine and modern humans – a feature which is intimately related to human-like bipedal gait with feet brought in midline under the body. The australopithecine femur is by far the most modern human like part of the postcranium (but not in relative length).

Arboreal locomotion

The main adaptations in australopithecine postcranial morphology which are attributed to arboreal locomotion are seen in the upper limb. In general, the upper limb proportions of australopithecines resemble those of great apes. The scapular morphology indicates a large degree of mobility in overhead motion of the shoulder and the thoracic spine indicates that shoulder muscles with spinal origin were large and presumably powerful. Phalanges are curved and relatively long. Knee- and hip joints probably had more degrees of mobility than in modern humans. Overall body proportions of australopithecines resemble great apes more than modern humans.

There is little doubt that the arboreal locomotor modes of australopithecines resemble those of great apes rather than cercopithecoid primates. Therefore it was probably forelimb dominated with hindlimb support in hauling the body up into the trees. Nevertheless, there is no consensus on the extent to which australopithecine arboreal

locomotion resembled that of African apes, Asian apes or was uniquely australopithecine (Latimer, 1991; Zuckerman et al., 1973).

The more modern human-like body proportions of *Homo ergaster* and its lack of distinctive adaptations to arboreal locomotion indicate that *Homo ergaster* was a habitual biped like modern humans and probably as successful as humans in climbing trees. This would mean that *Homo ergaster* certainly was capable of climbing a tree but probably rarely did so after childhood (just like modern *Homo sapiens*).

1.9 Functional anatomy of the lumbar spine

Although the vertebral column consists of a repetitive series of elements that look fairly similar, one also notices progressive differences in the shape of vertebrae along the column. For example, a cervical vertebra is easily discerned from a thoracic or a lumbar one. This is because changes in shape are usually continuous and differences in shape and function are manifested in small differences between neighbouring elements. These differences become more visible the farther apart two compared elements are.

1.9.1 Motion of the spine

The hominid spine is capable of flexion-extension in the sagittal plane, lateral bending, and rotation. Figure 1.14 illustrates these three motions in the human lumbar spine. Relative extents of the three motions vary between apes and humans. Additionally, the range of the three motions is different in each part of the spine. In humans, the degree of all three is highest in the cervical spine (Kapandji, 1992). The thoracic spine relative to the lumbar spine allows a high degree of rotation but is restricted in its flexion-extension motions due to the rib cage attached to the thoracic vertebrae. In the lumbar spine on the other hand, the flexion-extension mobility as well as the lateral bending mobility surpass the rotation mobility (Kapandji, 1992). In apes, the flexion extension-motion in the cervical spine is restricted due to elongated spinous processes (Schultz, 1961). Nevertheless, the cervical spine is the most mobile spinal region (in apes as well as in humans). In the thorax and lumbar regions, the ranges of motion of the spine compared to humans as well as cercopithecoids is highly restricted (Schultz, 1969a).

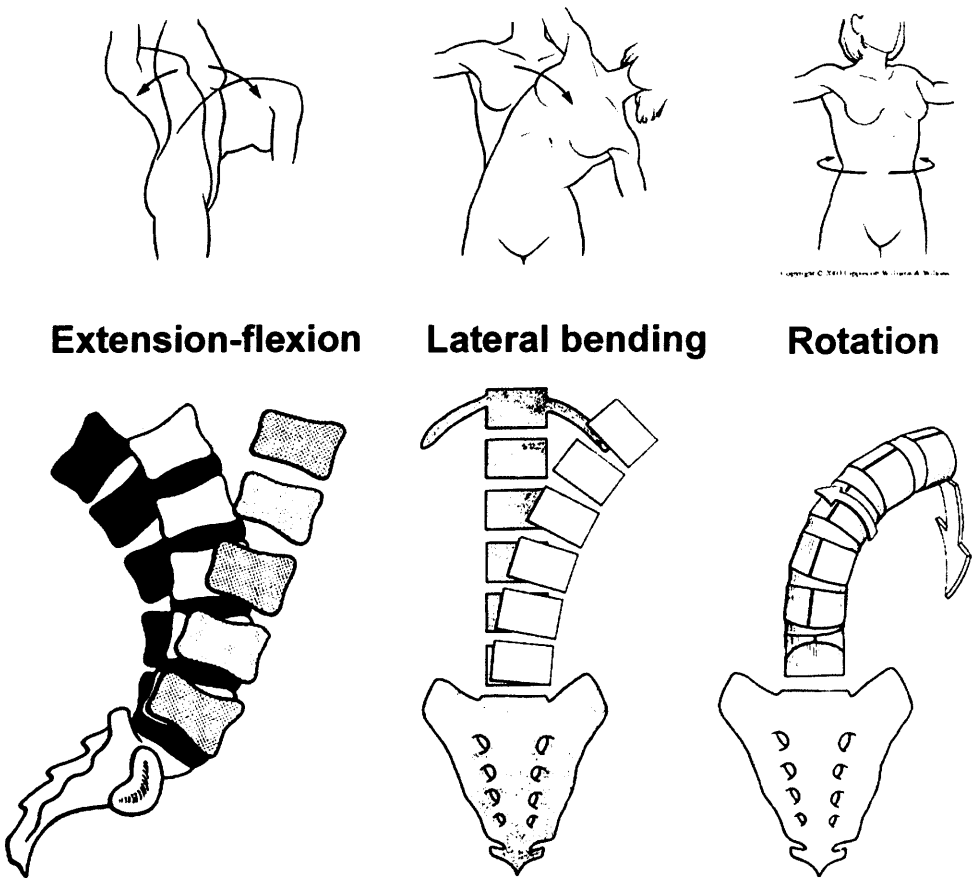


Figure 1.13 Motion of the human lumbar spine. Modified after Moore and Agur (2003) and Kapandji (1992)

1.9.2 Basic anatomy of the lumbar vertebrae

The lumbar vertebrae of both great apes and modern humans have no ribs attached to them and possess the same vertebral processes and anatomical features in general. Figure 1.15 shows a hominid (human) lumbar vertebra in superior (top) and left lateral view (bottom). In figure 1.15, all the anatomical parts relevant to this study are labelled.

1.9.3 Overview of spinal osteology

The hominid spine consists of between twenty-two and twenty-four presacral elements (Schultz, 1961). The total number of vertebrae can vary by one or even two within a given taxon. The number of lumbar vertebrae also varies, especially within the African ape taxa as will be discussed later in this chapter. Figure 1.16 shows the dorsal and anterior view of the human spine, which – except for the unique human lordotic and kyphotic curvatures (not seen in anterior and posterior view, for this see figure 1.5, p. 38

– is a typical hominid spine. The spine can be divided into three presacral regions; the cervical, thoracic and lumbar spine. Most caudally to the lumbar section is the sacrum, the region of the spine which connects to the pelvis and the cocygeal region.

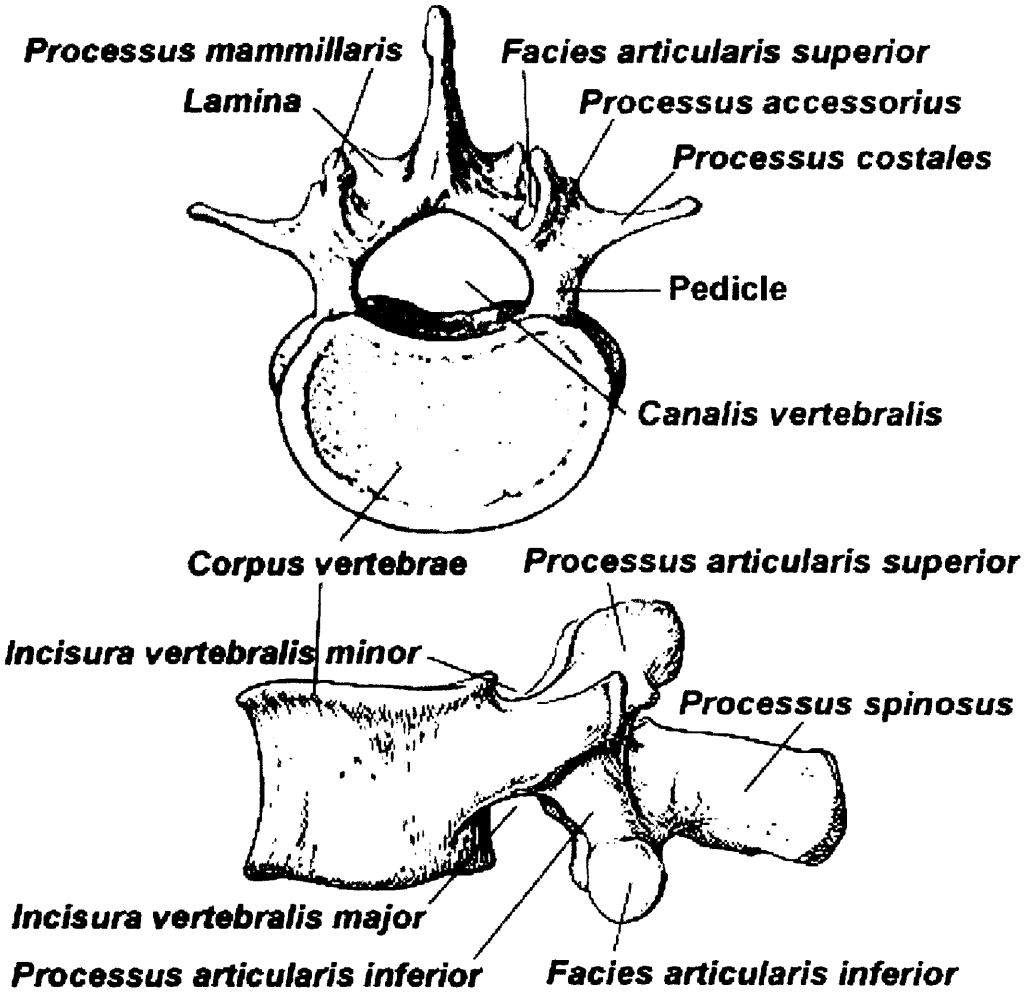


Figure 1.14 Anatomical features of a lumbar vertebra. Top: superior view, bottom: left lateral view. Modified after Platzer (1999)

The sacrum, in contrast to the presacral spine, is immobile and consists of fused vertebrae which give it a block-like appearance. In humans, motion can occur between the sacrum and pelvis but the degree of motion is small and individual differences are considerable. The motion of the iliosacral joints is of importance in child birth (Kapandji, 1992), increasing the diameter of the pelvic inlet crucially. However, in the great ape taxa, which have, compared to other primate taxa, rather small newborns, the pelvic inlet is strikingly larger than the head and shoulder breadth of newborns (Schultz, 1949). The ape sacrum is therefore less mobile than the human one - there is no necessity to enlarge the pelvic inlet during birth. After the sacrum follows the caudal

spine, which in all hominids including fossil forms is rudimentary; none of the hominid taxa has an externally visible tail (Schultz, 1961).

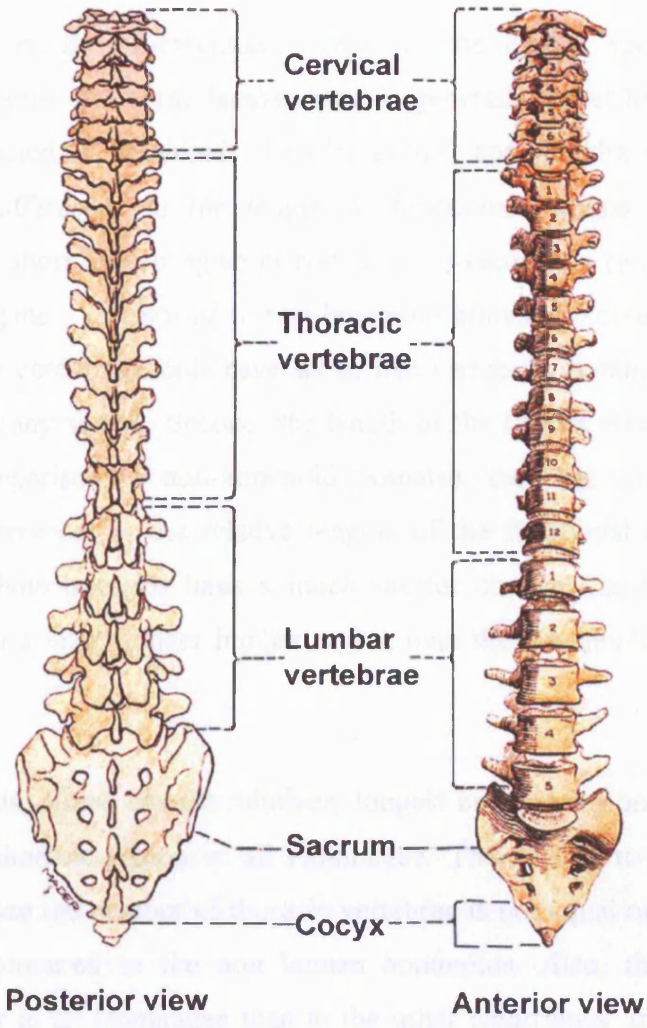


Figure 1.15 Vertebral regions in the human spine. From Agur (1991), p. 201

1.9.4 Spinal proportions

Superimposed over the segmental units of the spine are the regional units. In mammals, a cervical, thoracic, lumbar, sacral and caudal unit can be identified. The cervical spine, which connects the vertebral column with the skull, allows the head to be moved in all directions. This part of the vertebral column is therefore the most flexible. The next part is the thoracic spine, which forms the thorax and posteriorly provides an attachment platform for the ribs. This is usually the least flexible part of the spine since the movement of the vertebrae is restricted by the ribs. Flexion-extension mobility is small. However, the degree of rotation is bigger in the thoracic than in the lumbar spine. The

lumbar spine, finally, is relatively flexible and bears no ribs. Rotation movement is rather small, but the flexion-extension movement reaches high levels.

Among primates, the flexion-extension motion of the lumbar spine is considerably restricted in great apes. Thus, the lumbar spine is generally rather long in primates but considerably shortened in hominoids. Schultz (1961) and Schultz and Straus (1945) investigated the differences in the length of functional regions of the spine and concluded that the short lumbar spine in hominoids is caused by two factors. First, the hominoid lumbar spine – in contrast to non hominoid primates – consists of less lumbar vertebrae. Whereas cercopithecoids have six to five vertebrae, hominoids range from as few as two to as many as five. Second, the length of the lumbar elements is reduced in hominoids. In comparison to non-hominoid primates, they are considerably shorter. This results in differences in the relative lengths of the functional units of the spine. Non-human catarrhine primates have a much shorter cervical region, slightly shorter thoracic region and a much longer lumbar region than the hominoids including modern *Homo*.

Of all the hominoids, *Homo* has the relatively longest cervical region. Man also has the relatively longest thoracic region of all Hominidae. This is due to the longer human vertebral bodies since the number of thoracic vertebrae is not equal or may be decreased in *Homo* when compared to the non human hominoids. Also, the sacral region is considerably longer in all Hominidae than in the other catarrhines. In addition, gibbons are intermediate between great apes and humans on one side and the Cercopithecoidea on the other side. *Homo* is no different in the relative length of the sacral region when compared to the ape species. The increased length of the sacral region in apes and *Homo* is due to the increase in the number of sacral elements when compared to other catarrhines.

1.9.5 The number of vertebrae in different recent hominoid taxa

All primates have seven cervical vertebrae, a condition that they share with almost all orders of mammals (Schultz and Straus, 1945). Catarrhines usually have twelve thoracic vertebrae; however, the African ape taxa usually have thirteen (Schultz, 1961; Schultz and Straus, 1945). The Asian ape taxa differ in this condition: Gibbons usually have thirteen thoracic elements, whereas Orang-utans have twelve (Schultz, 1938; Schultz,

1961; Schultz and Straus, 1945). Except for the cocygeal/caudal region, the lumbar one is the most variable within the primates: in Cercopithecidae, there are usually six to seven lumbar elements. In the Hominoidea, including humans, there is a steady trend to reduction of the number of lumbar vertebrae. Gibbons and modern humans, with on average five elements, have the most, whereas only four, three or even two lumbar elements are common conditions with the African apes (Schultz, 1961; Schultz and Straus, 1945). The Orang utans are more stable in the lumbar region in that they mostly possess four lumbar elements.

In Cercopithecidae, the number of sacral elements is relatively stable at three elements. However, sometimes as many as four and as few as two vertebrae are counted (Schultz, 1961; Schultz and Straus, 1945). In African apes the number is variable between five and seven, depending on how many lumbar elements there are present. In Orang-utan and modern *Homo*, the number is more stable at four and five elements respectively. Gibbons usually have five or four elements (Schultz, 1961; Schultz and Straus, 1945).

1.9.6 The number of vertebrae in fossil hominins

To date, no complete vertebral column of a fossil hominin is known which would solve the debate about how many vertebrae there were present in the fossil hominin spine. However, under the assumption of parsimony some statements can be made based on observations in recent hominid taxa and mammals in general. First, it can be inferred that australopithecines, as well as *Homo sapiens* had seven cervical vertebrae since this number is astonishingly stable throughout the mammals. As for the thoracic spine, it is more difficult to be certain. All Cercopithecoids have twelve thoracic vertebrae, as in the *Hominidae* do *Pongo,* and modern humans. In contrast, *Hylobates*, *Gorilla* and *Pan* have thirteen thoracic elements. From the fossil evidence, it is unclear if australopithecines had either twelve or thirteen thoracic elements, since no complete thoracic spine has been recovered yet.

The commonly held view that fossil hominins had six lumbar vertebrae is mainly based on Robinson's interpretation of the partial *A. africanus* Sts14 skeleton (Robinson, 1972). His claim was later supported by the analysis of the almost complete *Homo ergaster* skeleton KNM-WT 15000 by Walker and Leakey (1993). In both fossils, six lumbar vertebrae have been described. However, *Homo ergaster* and Australopithecines

– although probably closely related – have different body proportions and postcranial morphology. Albeit, the most recently discovered (and available) *A. africanus* specimen Stw431, of which among other postcranial elements a partial vertebral column is preserved, Tobias (1992) and Benade (1990) described only five lumbar vertebrae. Nevertheless, they concluded that Robinson's hypothesis of australopithecines generally having six lumbar vertebrae was to be supported. They claim that the presence of six vertebrae must have been more common in *A. africanus* – due to "the high frequency of six lumbars" (Benade, 1990) in their sample size (n = 2).

This view has been challenged by myself and colleagues (Häusler et al., 2002). In our study, based on the re-examination of the fossils in question (*A. africanus* Sts14, *Homo ergaster* KNM-WT 15000) and supported by additional findings (*A. africanus* Stw431) we were able to show that Australopithecines, as well as *Homo ergaster* had five lumbar vertebrae as is the case in modern humans. Figure 1.17 illustrates the proposed evolution of the number of vertebrae in Hominoidea. Briefly summarised, our arguments against the hypothesis that fossil hominins had six lumbar elements are as follows.

In the re-examination of the *A. africanus* specimen Sts14, we could show that the sixth from last presacral vertebra, labelled Sts14f, has a thoracic type rib articulated to its left side. Since we considered vertebrae with one or two freely moveable ribs of the non-lumbar type as thoracic, this leaves Sts14 with five lumbar elements (Häusler et al., 2002). We defend this with the argument that free moveable ribs of the thoracic type are functionally relevant. We acknowledge that Sts14f is of transitional character, thus a decision as to whether australopithecines had five or six lumbar elements based solely on this specimen would be insecure. However, the hypothesis, that australopithecines had five lumbar elements gains further support from the re-examination of the specimen *A. africanus* Stw431. We could show that on the right – preserved side – of the vertebral body of the sixth from last lumbar element, Stw431q (formerly recognized as Th12), there are clear remnants of a rib facet (Häusler et al., 2002). Due to the fragmentary condition of the vertebra Stw431q, we cannot determine if there was a similar rib facet present on the left side. Since we also acknowledge a unilateral free moveable rib to determine a vertebra's character, we declare this vertebra to be the last thoracic one, thus Stw431 had five lumbar elements.

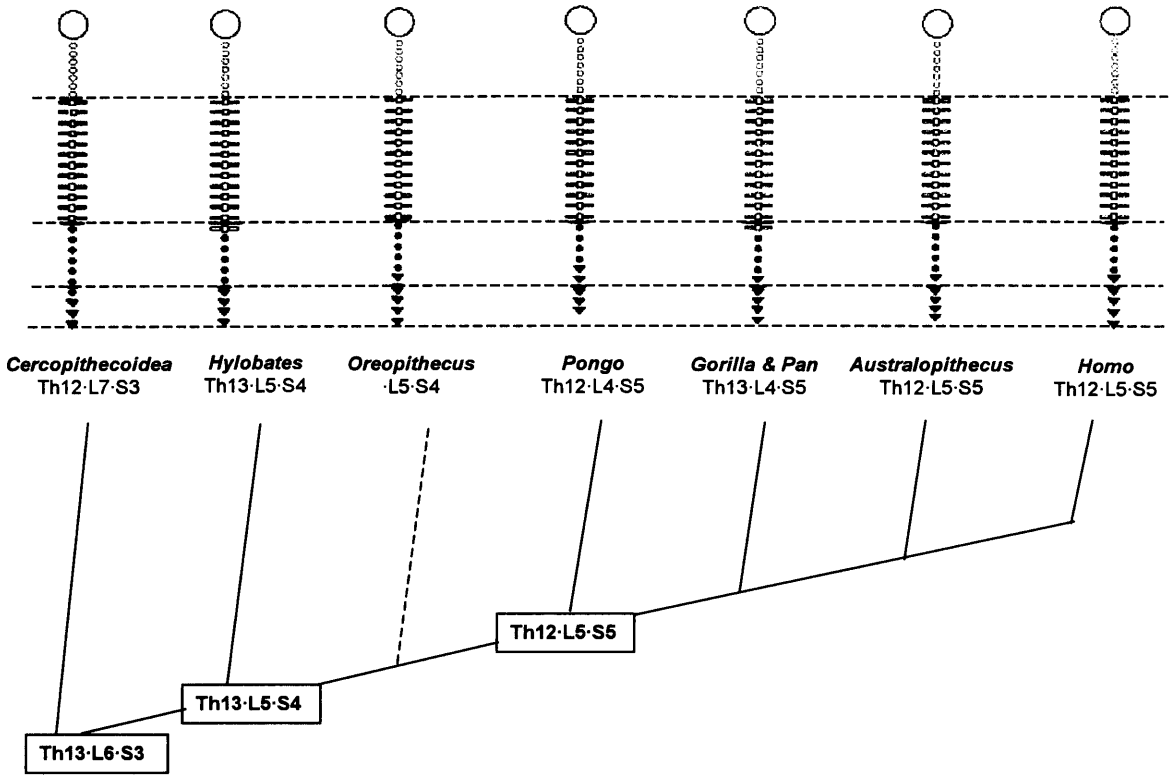


Figure 1.16 Diagram of a model of hominoid vertebral number evolution. After Häusler et al. (2002), p. 636

A careful re-examination of the *Homo ergaster* specimen KNM-WT 15000, led to doubts about the interpretation of the seventh from last presacral vertebrae by Walker and Leakey (1993). They postulated in counting six lumbar elements in this early hominin taxon, they assumed the last thoracic vertebra missing. Neither the metrics nor morphology of the vertebrae in the vicinity of the thoraco-lumbar border nor the orientation of the spinous processes strengthen this hypothesis of a missing vertebra. The simplest and most parsimonious interpretation is that the sixth from last presacral vertebra does not represent L1 but Th12 which is therefore not missing as suggested by Walker and Leakey (1993). Further support for our view of australopithecines having five lumbar elements stems from the fact that all fossil hominin sacra so far recovered (*Australopithecus afarensis*, AL288-1 and *Paranthropus robustus* DNH 43) consist of five vertebral elements like modern humans (Cook, 1983; Gommery et al., 2002; Johanson et al., 1982a). Therefore, our view suggests no changes occurred at the caudal end of the vertebral column throughout the phylogeny from Miocene primates to australopithecines. Shifts in the number of thoraco-lumbar elements could only occur on the cranial end of the spine and this has been shown to be unlikely (Häusler et al., 2002). In the case of *Pan*, *Gorilla*, and *Pongo*, we assume that they evolved a lumbar

spine consisting of four lumbar elements (on average) independently. Based on our study of the number of lumbar elements in recent and fossil hominoids, the present study will treat australopithecines and *Homo ergaster* as having five lumbar elements as is the condition for modern humans.

1.9.7 The hominoid lumbar vertebrae

In the following section, inter-specific differences in lumbar vertebral morphology as reported and summarized to date by other workers will be presented. This summary will serve as a basis for the comparative studies of the lumbar spine morphology between extant hominoids (Chapter III, IV) and between recent and fossil hominoids (Chapter V). A summary of adaptations of vertebral elements (e.g. vertebral bodies, pedicles, vertebral processes) is also presented to address differences in bone architecture between great apes and humans. This section is followed by a summary of differences between the attachments of muscles on the lumbar spine of humans and great apes. This addresses differences in mobility of the lumbar spine between humans and great apes due to muscle function. Where it was possible to find information on how the ligaments influence spine mobility, this is also mentioned in this section.

The 1st lumbar vertebra, all hominoids

The first lumbar vertebra articulates with the last thoracic vertebra. Its shape and anatomy are slightly different from other lumbar elements because its superior neighbour is a thoracic vertebra. Often, anatomical features manifest in typical thoracic elements are mixed with more typically lumbar ones in the first lumbar vertebra. In humans and great apes, commonly, the superior articular processes of the first lumbar element are very like those of thoracic vertebrae in size, shape and orientation. This means they have shorter superior articular processes than other lumbar vertebrae. The processes are also more horizontally orientated, and they have relatively larger, posteriorly orientated mammillary processes. Additionally, the articular facets are very flat and horizontally orientated. In contrast, the inferior articular processes and articular facets are more sagittally orientated and more elongated than thoracic ones. Further, the spinous process is often more caudally orientated than is common in other lumbar vertebrae (Schultz, 1961; Shapiro, 1990; Shapiro, 1993b).

The 3rd lumbar element, modern humans

The third lumbar vertebra of humans deserves closer attention since it is positioned like a keystone in the middle of the "arch" of the lumbar lordosis (Kapandji, 1992). An adaptation to this position is the robust vertebral arch of this particular vertebra because at this point, various muscles insert and originate. Arising from the iliac blades and the lumbar vertebrae, fibres of *Longissimus* are bundled here and insert principally into the costal processes of L3. Second, from the spinous process of L3 most fibres of *Spinalis* originate. Thus, L3 acts as "*Punctum mobile*" for *Longissimus* but as "*Punctum fixum*" for *Spinalis* (Kapandji, 1992). L3 is therefore the point where the largest degree of flexion and extension motion occurs in the human lumbar spine. In great apes - at least in chimpanzees - *Spinalis* originates from the last thoracic vertebra and inserts on the spinous processes of the first eight thoracic vertebrae (Th1-Th8) (Sonntag, 1924). This allows for more mobility in the thoraco-lumbar region and more control over the motion (increase and decrease) of the lumbar lordosis in the sagittal plane (Kapandji, 1992). Since great apes do not have a lumbar lordosis and since the position of *Spinalis* is different from *Homo*, there are no specific adaptations observed in the equivalent vertebra(e) equivalent to those of modern humans.

The last lumbar element, all hominids

The last lumbar vertebra articulates with a different functional segment of the spine, the sacrum. It has been widely noted that the last lumbar vertebra is set apart from other lumbars in size and shape. In humans, the last lumbar vertebra is submitted to the largest compressive loads. The whole weight of trunk, head, and upper limbs rests on it. Therefore, the last human lumbar has the largest vertebral body and its articular processes and zygapophyseal joints are specially adapted to resist shear stresses (Boszczyk et al., 2001; Slijper, 1946). In great apes, this vertebra is deeply embedded between the iliac blades and connected to them by strong iliolumbar ligaments. Here, this vertebra is rather immobile and various degrees of fusion (from partial to complete) with the first sacral vertebra (sacralization) are a fairly common condition (Schultz, 1938; Schultz and Straus, 1945). The last lumbar vertebra of great apes has – compared to their other lumbar vertebrae – a small and narrow vertebral body and the spinous process is short. The articular processes and joint facets are more narrowly spaced (Odgers, 1933; Shapiro, 1990).

1.9.8 Vertebral elements

As mentioned in the introduction to this section, differences in vertebral morphology between humans and great apes are related to differences in weight transmission and spine mobility. However, these two aspects of the role of the lumbar spine in locomotion are expressed in the size and shape of different vertebral elements: Differences in body weight transmission and spinal mobility are dictated by differences in bone architecture, ligaments, and muscles attaching to the lumbar vertebrae.

Vertebral bodies

From the upright trunk posture of modern humans, it follows that compressive loads are almost exclusively transmitted through the vertebral bodies and intervertebral discs, the pedicles, the articular processes and the vertebral arches, and the costal processes of the last lumbar vertebra (see also the section about the two column model of weight transmission, from p. 39) (Adams and Hutton, 1983; Boszczyk et al., 2001; Davis, 1961; Gracovetsky, 1986; Pal and Routal, 1987). Other workers have repeatedly pointed out that humans have disproportionally large single lumbar vertebrae when compared to great apes of comparable body weight. This has always been interpreted as an adaptation to resist relatively large compressive forces during the support of body weight with an orthograde trunk posture in relation to bipedal gait (Rose, 1975; Sanders, 1998; Schultz, 1953; Shapiro, 1993a; Shapiro, 1993b). Another adaptation to compressive load resistance through the upright lumbar spine is seen in the human inter-segmental pattern of size variation along the lumbar spine. Vertebral size increases steadily from L1 to L5. This again is interpreted as an adaptation to the cumulative effect of the load carried by the upright vertebral column which requires greater strength at its base (Odgers, 1933; Rose, 1975; Sanders, 1998; Schultz, 1953; Shapiro, 1993a; Shapiro, 1993b). Furthermore, in modern human lumbar vertebrae, especially the last one, varying degrees of posterior wedge shape are observed in the vertebral bodies e.g. (Rose, 1975; Sanders, 1998; Shapiro, 1990). The magnitude of the posterior wedge shape increases cranio-caudally along the spine. The wedge shape of the human lumbar vertebrae should be regarded in relation to the presence of a permanent lumbar lordosis (Amonoo-Kuofi, 1991; Sanders, 1998).

Pedicles

All hominoids (compared to non-hominoid primates) have thick and powerfully built pedicles which increase in size and diameter in the cranio-caudal direction (Davis,

1961; Panjabi et al., 1992; Rose, 1975; Shapiro, 1993a). The large pedicles of great apes and humans are interpreted as an adaptation to the transmission of large amounts of compressive loads between the vertebral bodies and vertebral arches (Pal and Routal, 1987; Shapiro, 1993a). Humans differ from the great apes in that there is a large increase in pedicle size and robusticity observed at the level of the last lumbar vertebra (L5 in humans) when compared to the level of the second last lumbar (L4 in humans) (Davis, 1961; Shapiro, 1993a).

Vertebral arches

The large size of the human vertebral arches also has been interpreted as an adaptation to load bearing in these structures. It has been estimated that, in modern humans, up to 20% of the total compressive loads transmitted through the lumbar spine pass via the vertebral arches, and the articular processes and zygapophyseal joints (Adams and Hutton, 1983; Kenesi and Lesur, 1985; Pal and Routal, 1987; VanSchaik, 1985). Additionally, in humans the amount of load transferred from the vertebral bodies to the vertebral arches of L4 and L5 is larger than that at the levels of L1 to L3. Thus, there is a marked increase in the size of vertebral arches observed in the last two presacral lumbars.

Articular processes and articular joint facets

The connecting bony elements between the vertebral arches of two consecutive vertebrae are the articular processes and facets (also often referred to as zygapophyseal joints and facets). The articular processes of all hominoids when compared to non-hominoid primates are long and strongly built (Sanders, 1998; Schultz, 1953; Shapiro, 1990; Ward, 1990). In humans, the distance between the articular facets increases cranio-caudally (Odgers, 1933). In great apes, on the other hand, it has been noted that this distance decreases. This is again seen in relation to the fact that the lumbar vertebrae of modern humans increasingly support more body weight the further caudally they are positioned.

The orientation of the articular joint facets is a good indicator as to the direction in which they predominantly resist forces (Adams, 1988; Boszczyk et al., 2001; Gal, 1993). In humans articular joints are adapted to resist shear stresses (Adams, 1988; Gracovetsky, 1986). Further, differences in the orientation and the size of the articular joint facets when compared to non-hominoid primates and when compared within the

hominoids indicate that their variation in modern humans and great apes can be interpreted as adaptations to weight transmission (Ankel-Simons, 1967; Odgers, 1933; Rose, 1975; Sanders, 1998; Schultz, 1961; Shapiro, 1993a; Shapiro, 1993b).

The orientation of the articular facets in modern humans provides a "safeguard" which prevents antero-caudal slipping of the vertebrae, especially the last lumbar one. The form of the facets, as well as how the inferior and superior facets of two consecutive vertebrae are interlocking with each other are good indicators for the degree of mobility of the lumbar spine of a particular species (Boszczyk et al., 2001). For example, the articular joints of horses have a tight, interlocking design, reducing the motion of the joints against each other but at the same time increasing the stability of the lumbar spine as well as its compression resistance abilities (Boszczyk et al., 2001; Kumar et al., 2002; Slijper, 1946). Humans, in contrast to great apes, have "loose" articular joints whereas the great ape joints are far tighter and interlocking (Martelli and Schmid, 2003). Figure 1.18 illustrates the tight interlocking of the superior articular processes and facets in chimpanzees compared to modern humans.

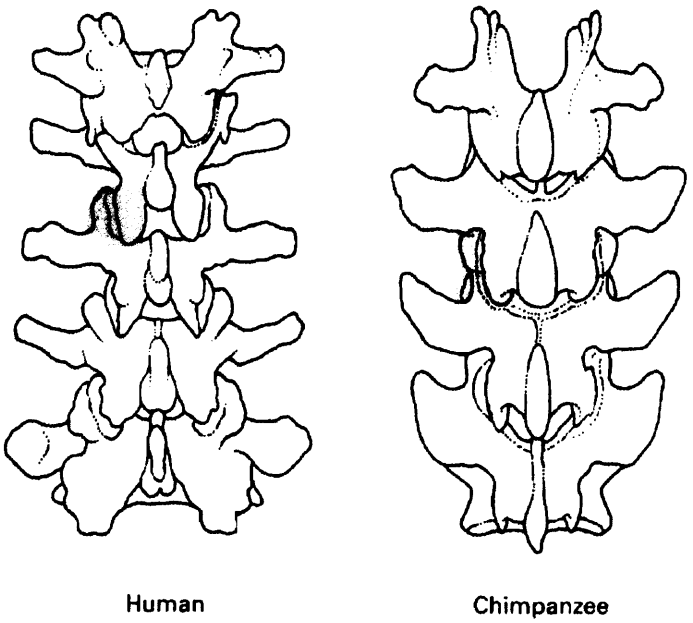


Figure 1.17 Articular joint morphology of humans and chimpanzee. Grey squares highlight articular joints. Note the distance between the superior border of the grey square and the inferior border of the costal process in modern humans and the absence of this distance in *Pan troglodytes*. Adapted from Aiello and Dean (1990), p 282

In relation to spine mobility and articular processes, it should be noted here that the larger mobility of two neighbouring vertebrae in modern humans is to no small part due

to large intervertebral discs (Gracovetsky, 1986; Kapandji, 1992). Kapandji (1992) reports the mean absolute height of the human lumbar discs to be at least 9 mm. Such thick intervertebral discs set neighbouring vertebrae farther apart from each other. As a consequence, human inferior articular processes are relatively longer compared to great apes to bridge the larger gap. The elongated arch and inferior articular processes, in combination with the large lumbar intervertebral discs, enhance the mobility of the lumbar spine in modern humans.

Costal processes

Costal processes provide attachment and origins for various back muscles which in turn partially define the mobility of the lumbar spine. In humans, especially *Longissimus* and *Spinalis* have fibres originating from these bony structures (Platzer, 1999). *Quadratus lumborum* and *Psoas major* are further muscles with extensive attachment to the costal processes (Platzer, 1999). The origin of the hominoid costal processes has a distinctive location dorsally on the root of the pedicles (Sanders, 1998; Shapiro, 1993b). In this, hominoids are clearly different from all other primate taxa. The costal processes are also dorsally orientated and considerably longer in hominoids than in other extant primates. Long, dorsally orientated costal processes provide long levers for powerful *Iliocostalis, Longissimus, Psoas major*, and *Quadratus lumborum* - especially when these muscles are contracted bilaterally (Shapiro, 1993b; Shapiro and Jungers, 1994; Shapiro and Simons, 2002). Additionally, the further lateral the tips of the costal processes lie relative to the axis of lateral flexion, the better are the leverages of *Iliocostalis* and *Quadratus lumborum* for lateral flexion when they are contracted unilaterally (Shapiro, 1990). Thus, the relatively long costal processes seen in the first two lumbar vertebrae of great apes serve as powerful levers in extension of the back. In great apes, these muscles are thought to help maintain their often displayed orthograde trunk posture (Shapiro, 1990; Slijper, 1946).

A specific adaptation to weight transmission functions of the lumbar spine has been observed in the costal processes of the last lumbar vertebra of great apes and humans. Pal and Routal (1987) point out in the latter that compressive loads resting on L4 are only partially transmitted through the vertebral body of L5 to the sacrum. They observed that vertebral body surfaces somewhat decrease between L4 and L5. Thus, compressive loads are alternatively transmitted through the costal processes and the iliolumbar ligaments of L5 (and L4). This assumption is underpinned by the

considerably increased size of the costal processes of the human last lumbar vertebra. The pattern of trabecular distribution and direction in the costal processes of L5 corroborates this assumption – at least in modern humans (Pal, 1989; Pal and Routal, 1987). The position and orientation of the iliolumbar ligaments themselves indicate that they are capable of transmitting tensile loads (Davis, 1961; Hartford et al., 2000; Kapandji, 1992; Pal, 1989; Pal and Routal, 1987).

Spinous process

Muscles that act on the spinous process in lumbar region are among others *Multifidus*. It inserts into the mammillary processes (Platzer, 1999). Its main action is the extension of the lower back and the stabilization of the trunk in bipedal gait of *Homo sapiens* e.g. (Macintosh et al., 1986). The generally square shaped and caudally inclined hominoid spinous process has been interpreted in relation to the importance of *Multifidus* acting on these processes (Slijper, 1946). It also has been argued that squared off spinous process with caudal orientation as seen in great ape taxa limit the mobility of single lumbar vertebrae against each other. In this context, the more horizontally (cranially) orientation of the lumbar spinous processes of modern humans should be seen in relation to greater degrees of extension possible in the lumbar spine (Shapiro, 1993b). Of all hominoid taxa, *Pongo* has very short spinous processes. The function of these is not entirely understood (Sanders, 1998).

1.9.9 Back musculature

Besides bony architecture, the ligaments and musculature contribute substantially to the stability (and mobility) of the vertebral column. It is not within the scope of the present study to explore the functional anatomy of the hominoid back muscles in relation to locomotor function: to achieve this, an extensive comparative study of the hominoid back musculature as well as quantitative approaches (biomechanics, in vivo etc.) would be necessary. Nevertheless, since the back muscles are intricately related to load bearing and spinal mobility and stability (Crisco and Panjabi, 1991; Mirka et al., 1997; Quint et al., 1998), differences between humans and great apes – as far as known – will be briefly introduced and summarized in the following section.

It has been reported that hominoids have broad *Erector spinae* muscles when compared to non-hominoid primates. This is due to their large body size and body weight, as well

as their distinctively very broad trunk (Ashton and Oxnard, 1975; Schultz, 1933; Slijper, 1946; Sonntag, 1924). Both humans and great apes have strong epaxial muscles, probably in adaptation to maintain the frequent, and in the case of modern humans habitual, upright body posture (Slijper, 1946). Nevertheless there are also differences observed in the epaxial musculature between modern humans and all great apes. The greater lumbar spine mobility of the human vertebral column requires tight control of motion between the lumbar vertebrae through the epaxial back muscles (especially the deep, small muscles) as well as the trunk muscles in general. This is to prevent spinal mobility impacting negatively on the overall stability of the spine. Unsurprisingly, (Slijper, 1946) reports differences in the strength and length of the longitudinal epaxial musculature in great ape taxa (namely *Gorilla*). In the latter, it is relatively thin and not as strongly built as in humans. Interestingly, the origin of the human *Iliocostalis* on the ilium and sacrum (via the thoraco-lumbar fascia) is narrower than in great apes and resembles other non-human primates (e.g. *Papio*) more (Swindler and Wood, 1982). The *Spinalis* of humans is also larger than in any great ape species. The differences in insertion and origin of *Spinalis* muscle have been explained previously, in relation with L3 morphology and function in modern humans (see p. 78). Figure 1.19 illustrates the differences in origin of *Spinalis* between humans and chimpanzees (blue arrows).

In contrast to modern human *Erector spinae* muscles, the great ape ones (especially *Longissimus* and *Ilicostalis*) have more extensive origins on the iliac crest (laterally) and sacrum and the insertions of *Longissimus* and *Spinalis* are farther cranially extended (Slijper, 1946; Sonntag, 1924). In general, the great ape epaxial musculature is thus characterized by less mobility in the thoraco-lumbar region (different origin and insertion of e.g. *Spinalis*). The musculature responsible for maintaining stability of the spine (e.g. *Seminspinalis* and *Multifidus* –especially in the lumbar region) on the other hand, is increased (Slijper, 1946).

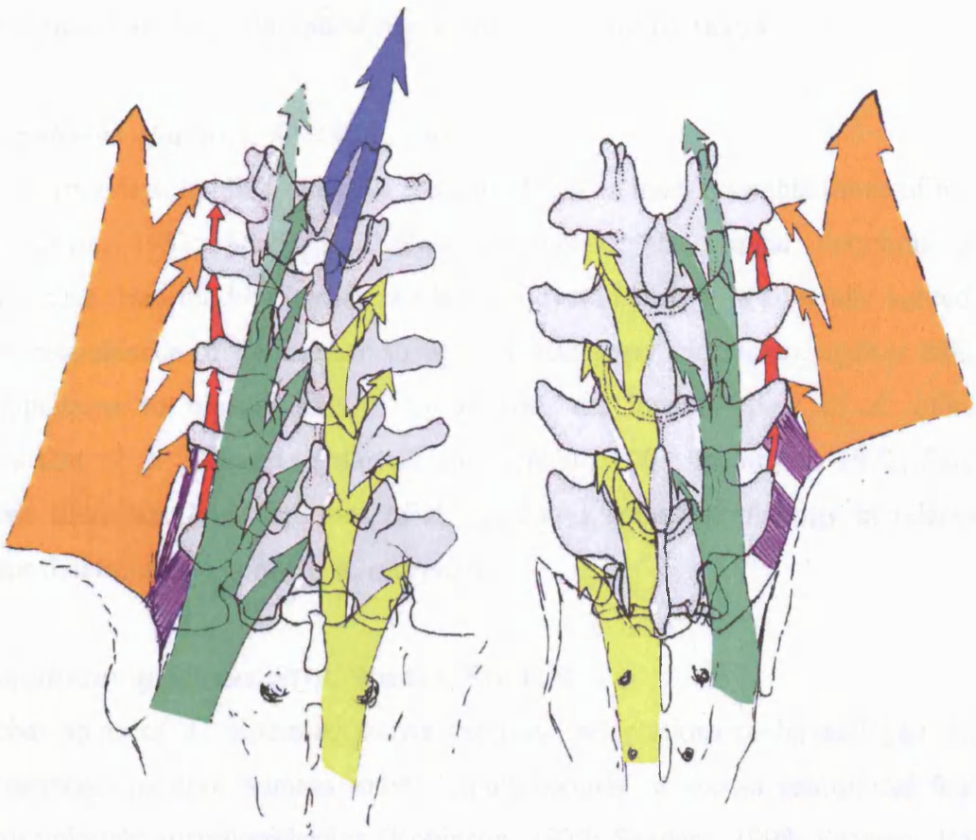


Figure 1.18 Muscles with origins and insertions on lumbar costal processes, the spinous process, mammillary processes and accessory processes of humans and chimpanzees. Origins of *M. spinalis* are also shown for *Homo sapiens*. Not shown: last ribs as insertions for *Quadratus lumborum* and the *Mm. interspinales*. ■ = *Quadratus lumborum*, ■ = *Mm. intertransversarii lumborum*, ■ = *M. multifidus lumborum*, ■ = *M. rotatores*, ■ = *M. spinalis*, ■ = *Ligg. lumbosacrales*. Adapted from Aiello and Dean (1990), p 282

1.9.10 The vertebral column in the fossil hominin record

This section will summarize current opinions on the morphologies and associated functions of fossil hominin vertebral remains. The emphasis is on australopithecines which are represented in the fossil record and included in this study. However, *Homo ergaster*, which is – based on its postcranium – considered to be a fully bipedal taxon is also discussed since the vertebrae of the Nariokotome skeleton (KNM-ER 15000) are also included in the study.

1.9.11 Summary of hominin spinal functional anatomy by taxon

***Australopithecus afarensis*, AL288-1, Lucy**

To date, *A. afarensis* lumbar vertebrae are considered to most resemble those of modern humans (Cook, 1983; Sanders, 1998). Nevertheless, the lumbar vertebrae of *A. afarensis* differ from modern human not least in overall size. It is generally agreed that the close resemblance of the lumbar spine of *A. afarensis* and *Homo sapiens* indicates their adaptations to bipedal gait(s). In general, the lumbar spine of *A. afarensis* resembles that of *A. africanus* (Martelli and Schmid, 2003; Robinson, 1972; Sanders, 1998) and therefore, interpretations of *A. africanus* spine morphology in relation to locomotor functions also apply to *A. afarensis*.

***Australopithecus africanus*, St14, Stw431, Stw41/8**

The lumbar spine of *A. africanus* shows extensive adaptations to bipedal gait; and in this it resembles modern humans most. Simultaneously, it shows anatomical features which are uniquely australopithecine (Robinson, 1972; Sanders, 1998; Shapiro, 1993a). These adaptations have been interpreted in relation to a different weight transmission mechanism through the lumbar spine of australopithecines when compared to modern humans.

***Homo ergaster* KNM-WT15000**

The lumbar spine of *Homo ergaster* resembles that of modern humans closely and therefore represents a habitual biped, additionally adapted to bipedal running (Latimer and Ward, 1993). The *Homo ergaster* lumbar spine (and the entire postcranium) shows no adaptations to arboreal locomotion.

1.10 The development of the axial skeleton in mammals

In this section, a brief overview is given of how the mammalian axial skeleton, its functional regions and the morphology of the different types of vertebrae are regulated during ontogeny. It is important to have an understanding of these mechanisms because it is during gastrulation - an early stage of embryonic development - that differences between taxa in the total number of vertebrae as well as in the numbers of vertebrae that make up a functional region of the spine are established. As will be seen, sometimes it takes only small changes in the expression of one or a few genes to change the total

number of vertebrae or the numbers of vertebrae that make up a functional region of the spine. Thus if small mutations can influence the length of the spine or functional regions of the spine by altering the number of vertebrae, and hence could alter the shape of the trunk and axial skeleton, this would serve well as an explanation for how the transition from an ape-type trunk (13 thoracic and 3 to 4 lumbar vertebrae) to a more hominin-type one (12 thoracic and 5 lumbar vertebrae) was orchestrated in a relative short period of time.

1.10.1 The organization of Hox genes and their expression in the formation of the axial skeleton of vertebrates

During gastrulation, the anterior-posterior axis is specified in all vertebrates by the expression of Hox genes. Hox genes belong to a family of regulatory genes expressed during ontogeny along the anterior-posterior axis in most metazoans (Burke et al., 1995). Hox genes are specified by having a homeobox. A homeobox is a DNA sequence about 180 base-pairs long and it encodes a protein domain, (the homeodomain) which can bind to DNA. The homeotic genes found in both flies and mammals are of the same general type. Additionally, the order of these genes on their respective chromosomes is remarkably similar (Kessel and Gruss, 1990).

Hox genes are organized in Hox gene complexes. The mouse and human genomes contain four copies of the Hox complex per haploid set. They are located on four different chromosomes (*Hoxa* through *Hoxd* in the mouse and *HOXA* through to *HOXD* in humans) (Greer et al., 2000; Ladjali-Mohammedi et al., 2001; McGinnis and Krumlauf, 1992; Scott, 1992). These complexes can further be discerned into 13 gene subfamilies, each containing several genes (*Hoxd1, 2,..., 12, 13*) (Carpenter et al., 1997; Fromental-Ramain and al., 1996; Krumlauf, 1994). The mammalian Hox/HOX genes are numbered from 1 to 13, starting from that end of each complex that is expressed most anteriorly (Burke et al., 1995; Kessel and Gruss, 1991). Hox genes code for transcription factors which typically switch on a whole cascade of other genes, for instance all the ones needed to form the body axis or a limb.

In the formation of the anterior-posterior axis, Hox gene expression is observed along the dorsal axis (neural tube, neural crest, paraxial mesoderm, and surface ectoderm), from the anterior boundary of the hindbrain through to the tail. The different regions of

the body from the midbrain through to the tail are characterized by different constellations of Hox gene expression and the pattern of Hox gene expression is thought to specify the different regions. This sequence of genes, acting at different locations and during different stages during morphogenesis is called the *Hox code*. The Hox code determines the identity of the anterior-posterior axis in that it specifies the identity of vertebrae (see later in this section) (Burke et al., 1995; Fromental-Ramain et al., 1996; Kessel and Gruss, 1991).

1.10.2 The formation of the somites

After the anterior-posterior axis of the embryo has been established, the trunk mesoderm is subdivided among other tissues, into the paraxial mesoderm, also called somatic dorsal mesoderm. Through the process of somitogenesis, the paraxial mesoderm is then further divided into whorls of cells called somitomeres. Most somitomeres develop further into discrete blocks of segmental mesoderm called somites (Liem et al., 2001). Although the mechanism controlling the periodicity of somite formation is not completely understood, one of the key agents in this process is the Notch signalling pathway (Dubrulle and Pourquié, 2002). The Notch signalling pathway also determines the number of somites that will be produced and this number is species specific (Richardson et al., 1998).

The first somites appear in the anterior portion of the trunk, and new somites "bud off" from the rostral end of the paraxial mesoderm at regular intervals. As the formation of the anterior-posterior axis follows a cranio-caudal direction, so does the somitogenesis. In humans, usually 42 to 44 pairs of somites form but these numbers are later reduced to 37 pairs of somites (Richardson et al., 1998).

1.10.3 The differentiation of vertebrae, muscles, and skin from somites

Although somites look identical, they will form different structures at different positions along the anterior-posterior axis. The somites give rise to most of the axial skeleton including the vertebral column with the ribs, parts of the occipital bone of the skull, the voluntary musculature of the neck, body wall, and limbs, and to part of the dermis of the neck and trunk (Christ et al., 2000; Gilbert, 2003).

Somites undergo considerable reconstruction when differentiating into vertebrae. One portion of the somites is called the sclerotome and cells rising from this portion will become the cartilage cells of the vertebrae and, in the case of the thoracic vertebrae, of the ribs.

The sclerotomes undergo resegmentation so that the segmental spinal nerves exit between the vertebrae (Afonso and Catala, 2003; Aoyama and Asamoto, 2000; Christ et al., 2000; Huang et al., 1996). This is achieved in that the sclerotomes split and recombine to produce the vertebral rudiments that lie inter-segmentally as will the vertebra that is produced by the vertebral rudiments. The sclerotomes split into a cranial and caudal half (see figure 1.20). The cranial half then fuses with the succeeding caudal half of the next sclerotome.

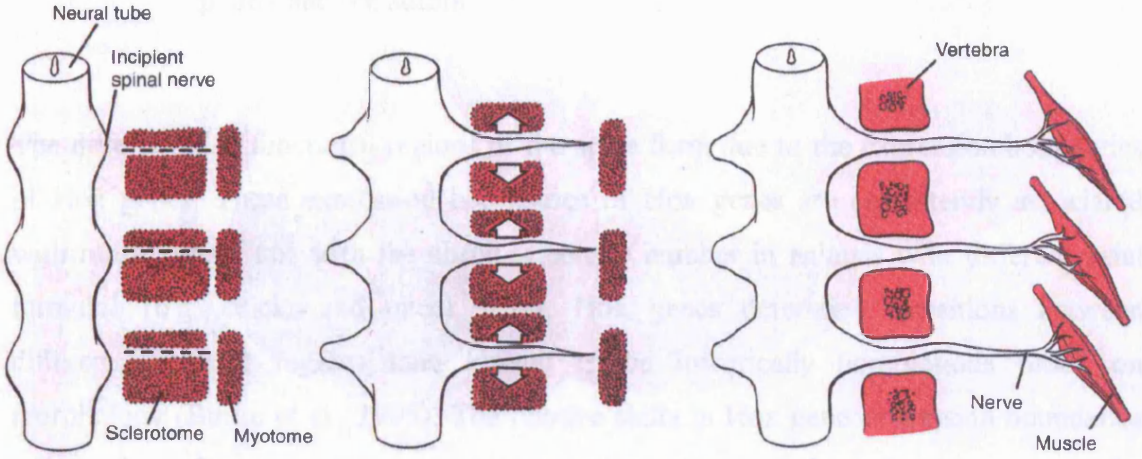


Figure 1.19 Scheme of recombination of vertebrae forming sclerotomes. Vertebral rudiments are formed through the recombination of a cranial sclerotome segment with the next caudal segment. Myotomes are enervated by segmental spinal nerves which grow out through the split in the original sclerotome. From Larsen (2001), p. 82

1.10.4 The differentiation of different types of vertebrae

As mentioned in section 10.1.2, the Hox code determines the type of vertebra that is formed through differences in Hox gene expression along the anterior-posterior axis (Burke et al., 1995). Or in other words: the Hox code determines the morphology of individual vertebrae (Kessel and Gruss, 1991). In mice and chicks, this explains why they have different numbers of vertebrae in each functional region of the spine but the same total number of vertebrae (Burke et al., 1995).

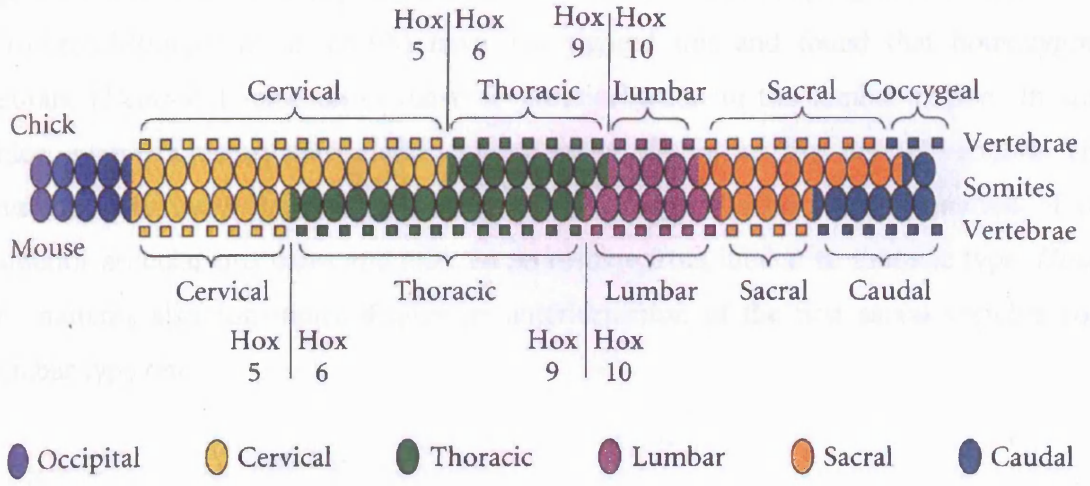


Figure 1.20 Schematic representations of the mouse and chick vertebral segmentation patterns as established by the expression of certain Hox gene paraloguous groups. From Burke et al. (1995) and further adapted by Gilbert (2003), p. 381 and the author

The differences in functional regions of the spine form due to the expression boundaries of Hox genes. These expression boundaries of Hox genes are consistently associated with morphology, not with the absolute somite number in animals with different axial formulae (e.g. chicks and mice). Thus, Hox genes determine transitions between different vertebral regions long known to be historically homologous based on morphology (Burke et al., 1995). The relative shifts in Hox gene expression boundaries reflect the relative expansion and contraction of morphological regions, e.g. the lengthening and shortening of thoracic and lumbar region between related taxa during evolution (Burke et al., 1995) (see figure 1.20). Differences in the length of functional regions of the spine are established by the number of vertebrae a functional unit consist of.

Recent investigations of Hox genes in studies of mouse development as well as in cross species studies of mice and chicks have enhanced our understanding of how these genes influence the character of functional regions of the vertebral column as well as of single vertebrae. For example, studies of Hox gene expression show that the expression boundaries of *Hoxa-9, Hoxb-9* and *Hoxc-9* are found in close association with the morphological transition from thoracic to lumbar vertebrae in mice and chicks (Cruz and al., 1999; Fromental-Ramain and al., 1996). The boundaries of *Hoxd-9* gene expression at the end of the lumbar vertebral series are followed by the expression of

genes of the *Hox-10* family in the initial segments of the sacrum (Burke et al., 1995). Fromental-Ramain et al. (1996) have investigated this and found that homozygotic mutant (*Hoxa-9*$^{-/-}$) mice often show an anteriorization in the lumbar region. In such mice, a supernumerary pair of ribs is produced on the former first lumbar vertebra. This vertebra also lacks the lumbar type costal processes. Further, the orientation of the superior articular processes and joint facets change from lumbar to thoracic type. *Hoxa-9*$^{-/-}$ mutants also sometimes display an anteriorization of the first sacral vertebra to a lumbar type one.

1.11 Thesis outlook

The following paragraphs summarize what possible results could be expected from each of the analysis sections of the thesis. These consist of Chapter III, intra-specific size and shape variation within modern taxa; Chapter IV, inter-specific size and shape variation between modern taxa; and Chapter V which is concerned with the comparison of modern and fossil taxa.

The studies in Chapter III are conducted because some of the recent hominoid taxa in the study (e.g. *Gorilla, Pongo*) show a considerable degree of sexual dimorphism in body weight and size whereas others show intermediate (*Homo sapiens*) or small (*Pan*) degrees. It is important to asses the relationship between sexual dimorphism in body weight and size and vertebral morphology because *Australopithecus* probably shows large degrees of sexual size dimorphism (Jungers, 1983; Lockwood et al., 1996; McHenry, 1991b). Thus fossil material might be more precisely interpreted if it is known how and whether sexual size dimorphism impacts on vertebral morphology. Based on the literature review presented here, it is to be expected that sexual dimorphism in body weight, and potentially in locomotor repertoires, will have a relationship with vertebral size and/or vertebral shape. Based on the large sexual dimorphism in body weight and size observed in *Gorilla* and *Pongo*, one would expect the largest degree of sexual dimorphism in vertebral size and shape in these taxa. In *Pan*, few differences in vertebral size and shape are expected to be manifest since there is little sexual dimorphism in body weight and size observed within this taxon. If and how differences in locomotor repertoires observed within the great apes (see background section Chapter III, fron p. 136) are related to differences in locomotion and body weight remains to be resolved. In the case of modern humans, an intermediate

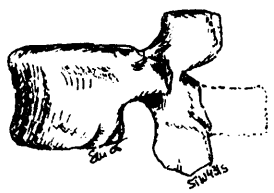
degree of differences in vertebral size and shape is expected based on the intermediate degree of sexual dimorphism in body weight and size when compared to great apes. In what way differences in bipedal gait has an influence on size and shape is not clear either. However, it would be expected to be rather small since both sexes engage in the same locomotor repertoires.

Chapter IV investigates inter-specific differences in vertebral size and shape between the modern taxa. Relationships between these and differences in body weight, locomotor repertoires, and phylogeny will be explored. In relation to the comparative studies of modern and fossil taxa, it is of interest to know how differences in body weight between the modern taxa influence the vertebral morphology between modern hominoids. Furthermore, the differences in locomotor repertoires (presence/absence of arboreal locomotor modes between humans and all apes) are highly likely to be expressed in the vertebral morphology. This will provide some clues about how to interpret the australopithecine vertebral morphology since the current consensus considers the australopithecine locomotor repertoire to consist of bipedal as well as arboreal locomotor modes.

With regards to inter-specific differences in body weight, it would be expected that *Gorilla* vertebral size and maybe shape differ most from all other taxa in the study, followed by *Pongo* males and both sexes of modern *Homo sapiens* and finally *Pan*. Differences in locomotor repertoires are expected to separate human vertebrae most from all other taxa since the human locomotor repertoire is the most distinct between all the modern taxa in the study. Between the great ape taxa, however, fewer differences are expected. If phylogeny has a strong relationship with vertebral size and/or shape, humans and *Pan* will show some close relationships since the currently favoured molecular based hominoid phylogeny places these two taxa closest together. Results to be expected from the analyses in Chapter V (comparison of modern and fossil hominoids) will be seen in relation to the results from Chapter III and IV. Thus, if the assumption that Sts14 is a female whereas the other *A. africanus* specimens in the study (Stw8, Stw431, and Stw572) are male is correct, then it should be expected that their vertebrae differ in size and shape similarly to those of *Gorilla* and *Pongo* since considerable sexual body weight and size dimorphism has been postulated for the australopithecine taxa (Jungers, 1983; Lockwood et al., 1996; McHenry, 1991b). In relation to locomotor functions, it should be expected that australopithecines resemble

humans most if bipedal gait contributed substantially to their locomotor repertoire. Where arboreal locomotor modes are still an integral and dominant part of the australopithecine locomotor repertoire, these are to be expected to leave their marks at least in vertebral shape. With regards to the early *Homo* species *Homo ergaster*, few differences in vertebral size and shape are expected if the current consensus interpretation of this taxon as a habitual bipedal runner and walker (similar to modern *Homo sapiens*) is confirmed (Bramble and Lieberman, 2004; Wang et al., 2004).

In the following thesis, the materials and methods employed will be introduced, followed by the three chapters which cover the investigation of intra-specific and inter-specific vertebral size and shape variation within and between recent hominoid taxa as well as the comparison of recent and fossil hominoid vertebral material. The results from these three chapters will be summarized in Chapter VI and discussed in relation to the reminder of the fossil hominin postcranium and the evolution of the hominoid vertebral column in general.



CHAPTER II MATERIALS AND METHODS

2.1 Introduction

In this chapter, the recent hominoid and fossil hominin vertebral material is introduced. In the present study, we use methods from the field of geometric morphometrics to a) collect and b) analyse three-dimensional landmark data from the five last presacral vertebrae of *Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*. These methods are summarized and introduced in this chapter. Further, statistical methods will be employed in consecutive studies (sexual dimorphism in vertebral size and shape, Chapter III, inter-specific differences in vertebral size and shape Chapter IV, and vertebral size and shape in fossil hominids, Chapter V) to assess the statistical significance of results. These methods too are introduced and summarized in this chapter.

2.2 Materials

2.2.1 Vertebrae

For this study, the forms of the last five consecutive presacral vertebrae of each specimen in the sample were recorded as sets of 62 three-dimensional bony landmarks. The landmarks were chosen to reflect the detailed form of each vertebra, hence their high density. The fifth from last vertebra was measured whether or not its morphology was lumbar or thoracic. The definition by Schultz (1961) and Schultz and Straus (1945) is used to define whether a vertebra is thoracic or lumbar. According to Schultz, a thoracic vertebra is "*the vertebra bearing ribs*". In the case of a vertebra bearing a true rib on one side but a costal process on the other (thoraco-lumbar transition), Schultz counts this vertebra as half thoracic and half lumbar. A lumbar vertebra, on the other hand, is

"*a vertebra between the thorax and the sacrum, bearing no ribs or possessing no lateral masses participating in the formation of sacral foramina*"

Measurements were taken consecutively, starting with the first free vertebra (i.e. not permanently attached to the sacrum and not taking part in forming sacral foraminae) from the sacrum and then moving in the cranial direction for the next four vertebrae.

2.2.2 Measurement criteria

Only specimens of known sex were chosen. All specimens in the sample were checked for pathologies before being considered fit for measurement. Those specimens with extensive osteo-arthritic growth (osteophytes) on the rims of the vertebral bodies or the zygapophyseal joint facets were not considered, except if the specimen was a rare fossil hominin. A vertebra was still included if it had a healed fracture that did not disrupt the overall shape of the vertebra in question. Only individuals with complete vertebral columns were considered.

2.2.3 Age estimation

All specimens were allocated to one of the following age groups: infant, juvenile, subadult, and adult. Information was usually provided by collection records; however, the following criteria were used to confirm this information:

Modern human specimens were considered adult if their postcranial skeleton was fully mature, meaning all epiphyses closed or closing thus visible in small traces only. For adult specimens from the Spitalfield collection, housed at the Natural History Museum, London, UK age at death was known from church records and coffin labels (Molleson et al., 1993). The complete immature human sample came from the Spitalfield collection and age estimations were provided by collection records, based on the analyses by Humphrey (1998) and sometimes supported by church records and coffin labels (Molleson et al., 1993). The specimens were classified as **infants** if their deciduous dentition was in the process of being completed. Thus, two specimens, aged 4.17 and 4.5 years belong to this age group. Specimens whose permanent dentition was in the process of being completed were classified as **juveniles**. The specimens belonging to this age group range from age 7 (youngest) to age 17.7 (oldest). Young adults/**subadults** were classified as specimens whose permanent dentition was complete yet their skeleton was not yet fully mature. The specimens belonging to this group were

aged between 18 and 25 years. **Adult** specimens (complete permanent dentition, mature postcranium) are 25 years of age and older.

The **great ape** specimens were considered to be **adult** if they possess the following features:

- The 3rd molars and the canines were fully erupted and occluded
- Limb bones showed only traces of the epiphyseal closure line and were fully fused
- Collection records (Powell-Cotton) and field notes by C. Bösch, available for the *Pan troglodytes verus* sample from the Taï National Park, Côte Ivoire confirmed the adult status of a particular specimen

They were considered **subadults** if they possess the following features:

- The 3rd molars and canines were erupting but had not yet reached full occlusion or final length
- The basilar epiphysis between the *Os sphenoidale* and *Os occipitale* was visible only in traces and other epiphyses still showed traces of incomplete fusion
- Collection records (especially Powell-Cotton) stated sub-adult. Usually this described individuals aged approximately 8 to 11 years of age in the case of *Pan* and *Gorilla* from the Powell-Cotton collection

Great ape specimens were considered **juveniles** if they possess the following features:

- The deciduous dentition was complete and one or more permanent teeth had already erupted
- The basilar epiphysis between the *Os sphenoidale* and *Os occipitale* was narrowly open or partially closed
- Limb bone epiphyses had started to close and the acetabular epiphyses of the pelvis were partially closed
- Collection records (Powell-Cotton) and field notes (Bösch) recorded juvenile status for a particular specimen

Finally, great ape specimens were considered **infants** if they possess the following feature:

- The deciduous dentition was in the process of completion
- The basilar epiphysis between *Os sphenoidale* and *Os occipitale* was wide open
- Limb bone epiphyses as well as the acetabular epiphyses of the pelvis were open
- Collection records (Powell-Cotton) and field notes (Bösch) stated infant specimen

In the great ape taxa, the age ranges attributed to the different age groups (infant, juvenile, subadult, and adult) are less easily identified than in humans. This is due to the fact that accurate age estimations for great apes in their natural habitat are relatively difficult to conduct e.g. Goodall (1986), Nishida et al. (1990), and Bösch and Bösch-Achermann (2000). Further it has been shown, that apes in captivity and apes in natural habitat mature rather differently (Bösch and Bösch-Achermann, 2000; Zihlman et al., 2004). However, great ape dental development indicates that all great ape taxa are dentally mature around the age of 11 years (Dean, 2000; Holly Smith et al., 1994). Based on studies of life history of chimpanzees in their natural habitat as well as dental development analyses of all great ape taxa (Bösch and Bösch-Achermann, 2000; Dean, 2000; Holly Smith et al., 1994; Nishida et al., 1990; Zihlman et al., 2004), apes are usually aged between 0 and 4 years when they belong to the group "infant". From age 5 to approximately 7, they are considered juveniles, whereas from age 8 to approximately 11 (depending on sex) they are adolescent (subadult). Adult great apes are usually older than 14 years.

2.2.4 Sample sizes

Whenever possible, the goal was to measure samples of at least 20 adult specimens per taxon. Ashton states that, empirically it has been found that 20 or more specimens almost invariably provide...

"an acceptably precise estimate of the means and variances of the population from which the samples have been drawn" (Ashton et al., 1971).

Where possible, this criterion has been applied also in measuring sub-samples (e.g. sex, age groups). In the following section, the origins of the vertebral material for each taxon sub-sample and the collections they come from are introduced.

Homo sapiens

The sample of modern humans comes from the collections of the British Museum (Natural History) and the collections of the Institute and Museum of Anthropology, University of Zürich, Switzerland. The total sample of modern humans consists of 58 specimens. Table 2.1 presents the total sample according to age and sex groups. Table 2.2 records single vertebral sub-samples. Both tables show that the immature sub-samples are not very balanced. This is because immature sexed human skeletal material is rare in collections. In all three immature age classes (infant, juvenile, and subadult) one sex is completely absent. With 11 specimens, the total immature sub-sample is small compared to the adult sub-sample (47 specimens). In contrast, the adult female-male ratio is relatively well balanced: 26 male and 21 female specimens.

The Spitalfields collection

The human material from the Spitalfields collection was retrieved during an excavation of the crypt of the Christ Church, Spitalfields (Commercial Street, Spitalfields, London E1) in 1985 (Molleson et al., 1993). Since then, the material has been housed in the British Museum (Natural History). The collection is of exceptional value because biological (age at death, sex) as well as socio-cultural (profession, social status) information is available for many of the specimens. This makes the Spitalfields collection one of the rare cases of an aged and sexed historic population available for research projects. The population is of European Caucasian background and dates to the late 18th and the 19th Century. People buried in the crypt of the church at Spitalfields were representative of the local population at the time. The entire immature sample in this study is drawn from the Spitalfields collection. Adults chosen from this population were chosen to adequately represent different ages (e.g. 20, 30, 40 etc years of age).

The Collections of the Anthropological Institute and Museum, University of Zürich, Switzerland

The collections contain the A. H. Schultz collection and the collection of the Anthropological Institute and Museum, University of Zürich, Switzerland. Part of the human material from these collections consists of contemporary (20th Century) skeletal material of Indian background which is used by the Institute as teaching material. The remaining human material is from the A.H. Schultz collection. This collection was created to represent various geographically specific variations of modern *Homo sapiens sapiens*. Thus, the present human sample contains (among others) two individuals from

Tierra del Fuego (South America), native North Americans, Americans of African descent, individuals from Russia (Tatars) and some from Birma (Southeast Asia).

Pan troglodytes

The sample of *Pan troglodytes* consists of specimens from collections housed at the Institute and Museum of Anthropology, University of Zürich and the Powell-Cotton Museum, Kent, UK. The total sample of *Pan troglodytes* consists of 85 specimens and is presented in table 2.1. The total immature sub-sample consists of 53 specimens and is larger than the total adult sub-sample (42 specimens). The adult sub-sample is approximately three quarters the size of the sub-adult sample. The female-male ratio over the total sample is almost one to one (45 females vs. 50 males). However, in the adult sub-sample, this ratio is somewhat skewed towards the female sex (24 specimens) when compared to the male sex (18 specimens).

Powell-Cotton Museum collection, Birchington-on-Sea, Kent, UK

The Powell-Cotton Museum, sited at Quex Park, Birchington-on-Sea, Kent was originally established to publicly display Major Powell-Cotton's vast collections of hunted and prepared African and Asian wildlife. He established his collection during his extensive expeditions to Africa and the Indian sub-continent. The collection contains large samples of *Gorilla gorilla* and *Pan troglodytes*. Because of the very accurate labelling system and record keeping used to catalogue the specimens, it is possible to track most individuals back to geographic localities. The collection records revealed that all specimens chosen for this sample were animals shot in the wild during the first half of the 20th Century from localities in modern day Cameroon, the Republic of Congo and the Democratic Republic of Congo (former Zaire). All specimens come from locations west of the River Congo and east of the Cameroon highlands, and therefore can be confidently assigned to the subspecies *Pan troglodytes troglodytes* (Jenkins, 1990).

The Collections of the Anthropological Institute and Museum, University of Zürich, Switzerland

The primate collections at University of Zürich consist of the A.H. Schultz collection and the primate collection which is continually extended. Both collections contain animals caught in the wild as well as zoo specimens. The two collections together hold approximately 6000 specimens, ranging from wet and frozen animals and parts of animals to skins and skeletons. The chimpanzee specimens in the collections of the

University of Zürich selected for this study are all wild animals which were collected from a population of chimpanzees living in the Taï National park, Côte Ivoire. These animals fell victims to an outbreak of Ebola (Formenty et al., 1999) and were collected by Bösch and co-workers who have studied these particular chimpanzee populations since 1979 e.g. (Bösch, 1995). All animals collected belong to the same local populations, thus they are homogenous in appearance and morphology. The chimpanzee population in the Taï National Park belongs to the subspecies *Pan troglodytes verus* (Jenkins, 1990). The sub-sample of *Pan troglodytes verus* consists of 12 animals, of which five are adults, three are sub-adults, 1 is a juvenile and 2 are infants.

Gorilla gorilla gorilla

The total *Gorilla* sample consists of 95 specimens (see table 2.1). The ratio of the immature to the mature sub-sample is about 4 to 5 which accounts for a balanced ratio (table 2.2). The female-male ratio of the adult sub-sample is approximately 3:4, which – because of the large number of specimens in total– is considered sufficiently balanced for further analysis.

Powell-Cotton Museum collection, Birchington-on-Sea, Kent, UK

All *Gorilla* specimens selected for this study were from the Powell-Cotton collection. The specimens were shot in the wild and accurately documented; therefore the locality can be traced back to modern day Cameroon, Gabon, the Republic of Congo and eastern parts of the Democratic Republic of Congo (former Zaire). The collection records indicate that all individuals came from west of the River Congo. Thus, all specimens can be assigned to the western lowland subspecies, *Gorilla gorilla gorilla* (Jenkins, 1990).

Pongo pygmaeus

The total *Pongo* sample consists of 21 specimens (see table 2.1). Of the recent taxa in this study, this was the smallest sample and it was limited by available collections and travel budget. The ratio of adult to immature specimens is about 3:4 (see table 2.2). The adult sample with a total of 12 specimens is way below the aimed at 20 specimens per sex. On the other hand, the sex-ratio is 1 to 1. The sample contained specimens from both sub-species *Pongo pygmaeus pygmaeus* and *Pongo pygmaeus abelii* as well as specimens of unknown subspecies. It is almost impossible to discern the two subspecies based on postcranial skeletal material. Because of these difficulties and because the

sample is small, no distinction between the sub-species is made in the present sample. The sample was collected from the Mammal collection, subdivision primate collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC USA and the collections of the Anthropological Institute and Museum, University of Zürich, Switzerland.

National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Most specimens (sixteen animals) of the *Pongo* sample came from the Mammal collection, subdivision primate collection of the National Museum of Natural History, Smithsonian Institution, Washington DC, USA. The records of this collection are very detailed. Based on the geographic information provided, five animals were identified as belonging to the sub-species *Pongo pygmaeus abelii* (the Sumatran sub-species). Eight specimens were from Borneo, hence belonging to the sub-species *Pongo pygmaeus pygmaeus*. The origin of the remaining three animals was undetermined but they were all caught in the wild and later died at the National Zoo, Washington DC, USA.

A.H. Schultz collection and Primate collection, University of Zürich

A further four specimens of *Pongo* shot in the wild specimens were available for measurement from the collections of the Anthropological Institute and Museum, University of Zürich. Of these four animals, one was from Sumatra and the other three were from Borneo.

Taxon	Infants	Juveniles	Sub-adults	Adults	Total
Gorilla gorilla	**16**	**16**	**6**	**57**	**95**
Pan troglodytes	**15**	**22**	**6**	**42**	**85**
Pongo pygmaeus	**3**	**2**	**4**	**12**	**21**
Homo sapiens	**2**	**7**	**2**	**47**	**58**
Total	**39**	**44**	**18**	**158**	**259**

Table 2.1 Total sample size of modern taxa (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus, and Homo sapiens*). Sub-samples are split into to age groups

Taxon	sex	Th13	L1	L2	L3	L4	L5
Gorilla gorilla	females	**8**	**8**	**8**	**8**	**8**	
infants	males	**8**	**8**	**8**	**8**	**8**	
Gorilla gorilla	females	**11**	**11**	**11**	**11**	**11**	
juveniles	males	**5**	**5**	**5**	**5**	**5**	
Gorilla gorilla	females	**3**	**3**	**3**	**3**	**3**	
subadults	males	**3**	**3**	**3**	**3**	**4**	
Gorilla gorilla	females	**33**	**31**	**33**	**33**	**17**	
adult	males	**24**	**25**	**26**	**24**	**18**	
Pan troglodytes	females	**10**	**10**	**10**	**10**	**11**	
infants	males	**15**	**15**	**15**	**15**	**14**	
Pan troglodytes	females	**9**	**9**	**9**	**9**	**8**	
juveniles	males	**13**	**13**	**13**	**13**	**14**	
Pan troglodytes	females	**2**	**2**	**2**	**2**	**2**	
subadults	males	**4**	**4**	**4**	**4**	**3**	
Pan troglodytes	females	**24**	**24**	**24**	**24**	**15**	
adult	males	**18**	**18**	**18**	**18**	**15**	
Pongo pygmaeus	females	**1**	**1**	**1**	**1**	**1**	
infants	males	**2**	**2**	**2**	**2**	**2**	
Pongo pygmaeus	females	**1**	**1**	**1**	**1**	**1**	
juveniles	males	**1**	**1**	**1**	**1**	**1**	
Pongo pygmaeus	females	**1**	**1**	**1**	**1**	**1**	
subadults	males	**3**	**3**	**3**	**3**	**3**	
Pongo pygmaeus	females	**6**	**6**	**6**	**6**	**6**	
adults	males	**6**	**6**	**6**	**6**	**6**	
Homo sapiens	females		-	-	-	-	-
infants	males		**1**	**2**	**1**	**2**	**2**
Homo sapiens	females		**4**	**4**	**4**	**4**	**4**
juveniles	males		**3**	**3**	**3**	**3**	**3**
Homo sapiens	females		**2**	**2**	**2**	**2**	**2**
subadults	males		-	-	-	-	-
Homo sapiens	females		**21**	**21**	**21**	**21**	**21**
adults	males		**26**	**26**	**26**	**26**	**26**

Table 2.2 Total sample size of lumbar vertebrae at each vertebral level for each modern taxon (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus,* and *Homo sapiens*). Samples are split into sex sub-samples

2.2.5 Fossil samples

Fossil hominin vertebral material is – in comparison to other skeletal parts – relatively rarely recovered. Of particular interest to the study are the fossil hominin taxa which are considered closely related to modern humans, such as the australopithecines (in this study: *A. africanus* and *A. afarensis*) and *Homo ergaster*. The taxonomy of fossil hominins is not resolved completely to date (Wood and Richmond, 2000). However, according to current views, australopithecines are considered close relatives of the

genus *Homo* and are therefore sampled for this study as was *Homo ergaster*. The latter is indeed considered a member of the genus *Homo*. Another candidate for data collection would have been *Homo sapiens neanderthalensis*. Although vertebral material exists e.g. (Arensburg et al., 1985; Boule, 1908; Capitan and Peyrony, 1909; Carretero et al., 2001) there was neither time nor financial resources available to sample this material. Photographs of all casts used in the present study are presented with catalogue number in the appendix.

All measurements for fossil hominins were taken from casts (cast materials and reconstructions of casts are presented in the appendix) except in the case of the *A. africanus* specimen Sts14, where the measurements for the first four lumbar vertebrae (L1 to L4) were taken directly from three-dimensional reconstructions of CT-scans (for details see the method section of this chapter). In the case of the last lumbar vertebra of *A. africanus* Sts14, a cast was available, thus measurements were also taken from the cast. The methods used to collect three-dimensional data required the specimens to be fixed in a stable position. Some of the fossil specimens are too brittle to be fixed in a steady position properly hence the use of casts was mandatory in some cases.

2.2.6 Reconstructing fossil vertebrae

Some of the vertebrae were partially damaged and missing some parts requiring reconstruction because the geometric-morphometric methods used require complete sets of landmarks for each specimen. These could have been estimated statistically (using means of extant taxa) but it was considered more secure to estimate via reconstructions based on available bony features and anatomical knowledge given that extant taxa are not necessarily good analogues for fossils.

Reconstructions were made in plasticine and Bostik Blu-Tack®. Both materials were later easily removed from the casts without leaving traces. As for damaged paired processes and zygapophyseal joint facets, it was often the case that, while one was gone (e.g. a costal process was missing), the second was still present. In such cases, measurements were taken from the surviving structures and reproduced for the missing piece. With regard to the vertebral bodies, the general contours of undamaged regions were used to define reconstructed structure. The appendix contains illustrations of each reconstructed fossil vertebra. In the following section, the fossil material is introduced

according to current taxon affinity. Figure 2.1 show a map of Africa, depicting the locations of the fossil hominin material investigated in the present study.

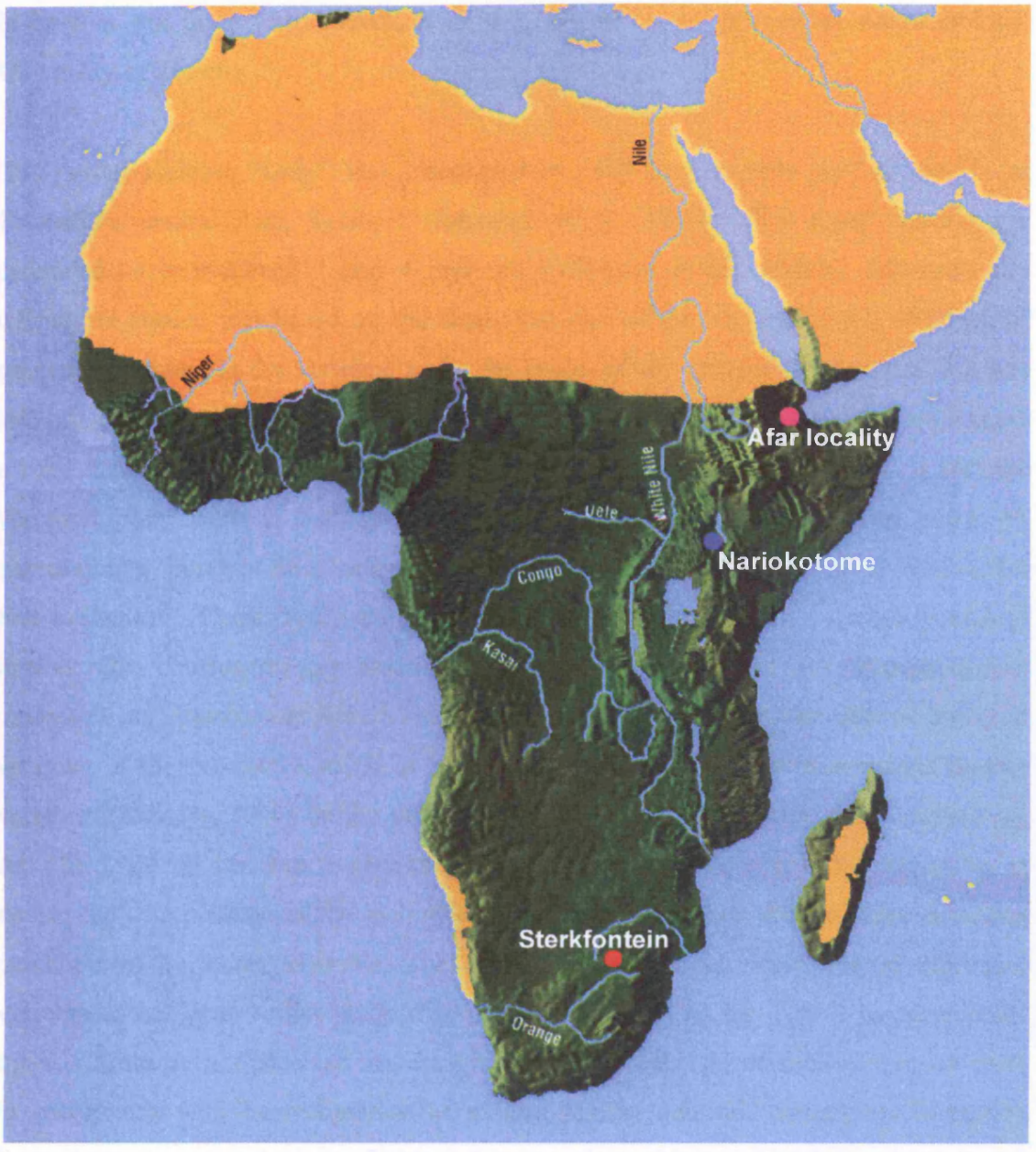


Figure 2.1 Map of locations of fossil hominin vertebral material. ● = *A. afarensis*, ● = *A. africanus*, ● = *Homo ergaster*. Adapted from Rowe (1996)

Australopithecus afarensis

The *A. afarensis* sample consists of a single lumbar vertebra which was recovered as part of the partial skeleton A.L. 288-1 (Lucy). The lumbar vertebra originally consisted of three fragments (A.L.288-1aa, A.L.-1ak, and A.L.288-1al). However, these

fragments fit together so well, that they were reconstructed to a complete vertebra, which only lacks the costal processes (Johanson et al., 1982a). All measurements of the *A. afarensis* lumbar vertebra came from an accurate cast (taken from the original fossil), housed in the fossil cast collection of the Institute and Museum of Anthropology, University of Zürich.

The partial skeleton "Lucy" was discovered in 1974 in the upper part of the Hadar Formation, central Afar, Ethiopia (Johanson et al., 1982a). The fossil remains are estimated to be between 3 and 4 myr old (Johanson et al., 1982b). Johanson and colleagues argued that based on the shape and size of the vertebral body, the lack of posterior wedging in the vertebral body, the length of the spinous process, and the size and orientation of the zygapophyseal processes and facets, this vertebra was most likely a third lumbar one. The only feature that is somewhat contradictory to this is that the vertebral body is very distinctly kidney-shaped – something that would rather be expected in a fourth or fifth lumbar vertebra (at least in a modern human). Contra to this first evaluation, (Cook, 1983) argues that she can identify the same vertebra as second lumbar. Her conclusions are based on the argument that... *"the inter-zygapophyseal diameters are appropriate for L2 relative to body size"*. Further, the lack of posterior wedging of the vertebral body is in her opinion only compatible with a second lumbar vertebra. (Sanders, 1994) on the other hand opted for a compromise and identified the AL 288-1 lumbar vertebra to be either L2 or L3. He considered it to be impossible to decide the true position of the incompletely preserved vertebra without more surviving neighbouring vertebrae available. The author of the present study treated this same vertebra as L3 in an earlier study (Martelli and Schmid, 2003). This is because in the opinion of the author, size and vertebral morphology of this particular vertebra are more in accordance with its recognition as a third lumbar and this assumption is carried through to the present study. Table 2.3 summarizes the sample of *A. afarensis* and indicates which landmarks needed to be reconstructed in order to sample the complete set of landmarks. The reconstruction of this vertebra is illustrated in appendix (pp. 389-406, figures A1 and A2).

specimen	vertebra	reconstructed landmarks
AL288-1	probably L3 or maybe L2	29, 35

Table 2.3 Sample size *A. afarensis*. Reconstructed landmarks indicate that the costal processes are missing

Australopithecus africanus

Most of the fossil vertebral material in this study is attributed to *A. africanus*. All *A. africanus* vertebrae in the study are from Sterkfontein whose principal site is the remains of a large collapsed cave near Johannesburg, South Africa. This site has yielded an astonishing amount of fossil hominin remains. The vertebral material from Sterkfontein is attributed to four different specimens labelled Sts14, Stw8, Stw431, and Stw572. Measurements from these four specimens were taken from casts housed in the fossil collection of the Institute and Museum of Anthropology at University of Zürich. The measurements of *A. africanus* **Sts14** were taken from an accurate cast of the original fossil for L5 and from CT-scans of all lumbar vertebrae of the original fossils (see appendix, pp. 389-406, figures A3 to A7). Shortly after discovery, the original fossils were reconstructed permanently with a gypsum-like material (Robinson, 1972). Due to the brittle condition of these bones, it is impossible to remove these additions. Modern human material was used as reference when these vertebrae were reconstructed. Their close resemblance to modern human vertebrae may therefore be overemphasized. The extent to which this will influence results of comparative analyses is yet to be seen. The complete lumbar vertebral series of Sts14 was discovered together with other bony material of a partial skeleton attributed to *A. africanus* which at the time of its discovery was the most complete single individual of an early hominid (Robinson, 1972). The bones were excavated in 1947 by Broom and Robinson (1947). The stratigraphy and sedimentation of the cave system of Sterkfontein is highly complex and difficult to untangle. Nevertheless, all specimens of *A. africanus* derive from a sediment layer called Sterkfontein Member 4, which probably dates to between 2.8 and 2.4 my (Partridge et al., 1991). Robinson (1972) noted some traits such as incompletely fused epiphyses between sacral vertebrae in Sts14. These were further investigated by Berge and Gommery (1999) who conclude that Sts14 is to be addressed as subadult with regards to sacral and pelvic morphology. They nevertheless agree with Robinson that for other postcranial parts, Sts14 can be addressed as (young) adult. Häusler (2001) supports this view. In as much the subadult age of Sts14 is influencing lumbar vertebral shape is to date not clear. However, this should be taken into consideration later in the thesis when results concerning this specimen will be discussed.

All measurements for *A. africanus* specimen **Stw431** were taken from accurate casts of the original fossils, housed in the fossil cast collection of the Institute and Museum for Anthropology, University of Zürich. *A. africanus* The vertebrae have not been

permanently reconstructed and are more or less in good shape. However, some of them, especially L1, L4, and L5 needed reconstruction (see appendix, pp. 389-406, figures A8 to A12). Stw431 is another partial *A. africanus* skeleton, although not as "complete" as Sts14. However, this specimen too has a complete lumbar vertebral series. Stw431 was recovered from Sterkfontein Member 4, Bed B, of the Sterkfontein formation in the field excavation campaign from 8th September 1986 to 30th June 1987. All australopithecine material from Sterkfontein is attributed to *A. africanus* (Benade, 1990; Day, 1986; Partridge et al., 1991). A brief description of the partial skeleton is given by Toussaint et al. (2003). The specimen appears to be fully mature and can be addressed as adult.

The third specimen **Stw8** is an incomplete series of fully adult lumbar vertebrae which has been assigned to *A. africanus* by Tobias (1973). Measurements for Stw8 were taken from an accurate cast from the original fossil, housed in the fossil cast collection of the Institute and Museum for Anthropology, University of Zürich. The lumbar vertebral series Stw8 consists of four lumbar vertebrae, firmly held together by matrix. Although the exact location of the specimen is unknown, the adherent matrix indicates that it derives from a Sterkfontein Member 4 deposit (Oakley et al., 1977). Sometimes, the specimen is referred to as Stw8/41. This is because a second partial vertebral series (StwH41), consisting of two articulated thoracic vertebral bodies was found in 1975 in Dump 18 in Sterkfontein by Tobias (Oakley et al., 1977). Based on concordance of size, shape, state of preservation, colouration, and matching areas of damage the two pieces are considered to form a continuous thoraco-lumbar series, probably from Th11 to L4 (Sanders, 1998; Tobias, 1978). The vertebrae are fixed in a kyphosis, probably due to post-mortem shrinkage of the anterior longitudinal ligament (Sanders, 1998). Only the second lumbar element of the series was preserved well enough to allow a reconstruction which was then measured. Although the four vertebrae are, as mentioned above, caked together by matrix, it was possible to measure all 62 landmarks on it with the MicroScribe. For a view of the reconstruction see appendix , p. 395, figure A13.

The fourth *A. africanus* specimen, **Stw572**, consists of a single adult lumbar vertebra which has been identified as probably being an L4 (according to the fossil hominid catalogue entrance, collection of the University of the Witwatersrand, Johannesburg). No further information was available as to why this vertebra has been identified as a fourth lumbar. The shape of its vertebral body and the orientations of its zygapophyseal

processes and joints do not contradict this interpretation. The vertebra was discovered in Sterkfontein Member 4, during the field excavation campaign of October 1984. Figure A14, p. 396 in the appendix shows this vertebra.

Table 2.4 summarizes the *A. africanus* sample and indicates which landmarks on which vertebra were reconstructed. Pictures of all *A. africanus* vertebrae that were reconstructed are shown in the Appendix. The issue of identifying the number of lumbar vertebrae in Sts14 and Stw431 is addressed in Chapter I, introduction (from p. 73)

Specimen	vertebra	reconstructed landmarks
A. africanus Sts14e	L1	All, CT scans used for reconstruction
A. africanus Sts14d	L2	All, CT scans used for reconstruction
A. africanus Sts14c	L3	All, CT scans used for reconstruction
A. africanus Sts14b	L4	All, CT scans used for reconstruction
A. africanus Sts14a	L5	11-13, 19, 20, 24, 37, 49, 50, 52-56, 58-62
A. africanus Stw431r, qa/qb	L1	25, 27-29, 33-46
A. africanus Stw431s	L2	12, 13
A. africanus Stw431t	L3	9, 12-14, 22, 23, 27-32, 34-36, 49-51
A. africanus Stw431u	L4	9, 23, 24, 27-32, 35, 39-42, 47, 48, 58-62
A. africanus Stw431v	L5	5-8, 10, 12, 13, 18-21, 25, 26, 33-38, 43-46, 48-50, 57-62
A. africanus Stw8	L3?	9, 12, 13, 27-32, 35, 39-42, 47, 50, 51-55
A. africanus Stw572	L4 or L3	5-7, 12, 13, 19, 23, 28-33, 35-37, 39-42, 50, 53, 54

Table 2.4 Sample size *A. africanus* and reconstructed landmarks

Homo ergaster

The *Homo ergaster* sample consists of a series of four lumbar vertebrae. All vertebrae measured belong to the same specimen, KNM-WT 15000. All measurements for *Homo ergaster* were taken from accurate casts of the original fossil. The casts are from the

fossil cast collection housed at the Institute and Museum of Anthropology, University of Zürich. The specimen was discovered at the Nariokotome III location, Northern Kenya (Walker and Leakey, 1993). The second lumbar vertebra survived in a state too fragmentary to perform a satisfactory reconstruction. The *Homo ergaster* sample thus contains only four vertebrae. Note, that in table 2.5, second column, the labelling of the vertebrae has been altered according to the results of the study by Häusler and the present author (2002). In this study, the lumbar vertebrae will be referred to according to this new interpretation. Figure 2.1 shows a map of Africa, depicting the locations of the fossil hominin material investigated in the present study. All four vertebrae are shown in the appendix, pp. 389-406, figures A15-A18.

Specimen	**vertebra**	**reconstructed landmarks**
Homo ergaster KNM-WT 15000 AV, AA	L2 new: L1	3, 4, 6, 7, 10, 12, 13, 20, 21, 27, 29-33, 35, 50, 58-62
Homo ergaster KNM-WT 15000 AB	L3 new: L3	2-7, 10, 20, 29, 33-35, 43-46
Homo ergaster KNM-WT 15000 BM	L4 new: L4	2, 15, 18, 29
Homo ergaster KNM-WT 15000 AC	L5 new L5	none

Table 2.5 Sample size *Homo ergaster*. L2 was too fragmentary to be reconstructed for sampling. New labelling of *Homo ergaster* vertebrae according to definitions by Häusler et al. (2002)

2.3 Methods

In the following sections, the measurement techniques as well as the statistical techniques will be explained and described. The geometric-morphometric methods will be generally introduced.

2.3.1 Choice of landmarks

In evolutionary biology, a special type of equivalence – homology - forms the basis of most comparative studies. The term homology relates to the matching of parts between organisms according to common evolutionary (and usually developmental) origin e.g. (Lieberman, 1999). In order to compare vertebrae, landmarks were chosen to represent overall shape and anatomical features which could be identified and compared in all

hominoid taxa in the study. To reflect the highly complex three-dimensional shape of lumbar vertebrae it was necessary to choose landmarks with a fairly high density. Concentrating on overall vertebral size and shape represents a new way to compare the morphology of lumbar vertebrae and is somewhat in contrast to earlier studies, where measurements were concentrated on specific anatomical features, e.g. the dimensions of the vertebral body as in studies by Benade (1990), Martelli and Schmid (2003), Rose (1975), Sanders (1998), and Shapiro (1993a).

2.3.2 Types of landmarks

A landmark is a point of correspondence on each object that matches between and within populations (Dryden and Mardia, 1998). Correspondingly, an anatomical landmark is a point assigned by an investigator that corresponds between organisms in some biologically meaningful way. Biological landmarks are often classified further. The landmarks used in this study were chosen according to the system of classifying them by Bookstein (1991) and further used and put under test by others, e.g. (Dryden and Mardia, 1998; O'Higgins, 2000). The classification of biological landmarks is mainly based on how powerfully they represent developmental or evolutionary homologies between taxa. This is for the most part of theoretical interest because it particularly imparts a sense of security of homology. Nevertheless, all landmarks are treated equally in the final analysis. It should also be noted that in the present study, many of the landmarks classed as Type III are not secure in their homology but are functionally equivalent – and this important in the context of this study of vertebral evolution and functional adaptation.

Type I landmarks

These landmarks represent points in space where three structures (histological), e.g. sutures or tissues meet. They most strongly represent evolutionary and developmental homology. Examples include the meeting of the sutures of the skull or the epiphyses of the pelvis (Bookstein, 1991).

Type II landmarks

This type of landmark is defined by geometric but not histological or local evidence. Further, this type of landmark might not be homologous in an evolutionary sense but is functionally equivalent. A good example would be the tip of a costal process or the margin of an articular facet. Support for homology is strong but not as strong as in case of type I landmarks (Bookstein, 1991).

Type III landmarks

These landmarks can be reliably located to an outline or surface of a structure but lack the specific location as seen in type I and II landmarks. An example would be the most anterior point on the rim of the vertebral body. The support of homology is weak for type III landmarks although functional equivalence is more secure (Bookstein, 1991).

2.3.3. Definition of landmarks in the study

In the present study, only Type II an III landmarks were used since there are no type I landmarks identifiable on vertebrae. Table 2.8 summarizes the 62 landmarks selected to represent the form of a single lumbar vertebra. The numbers of landmarks correspond with the order the landmarks were sampled on the bone. For better understanding it is recommended to compare the landmark definitions of table 2.8 with the illustration of these landmarks in figure 2.2 (location of each of the 62 landmarks).

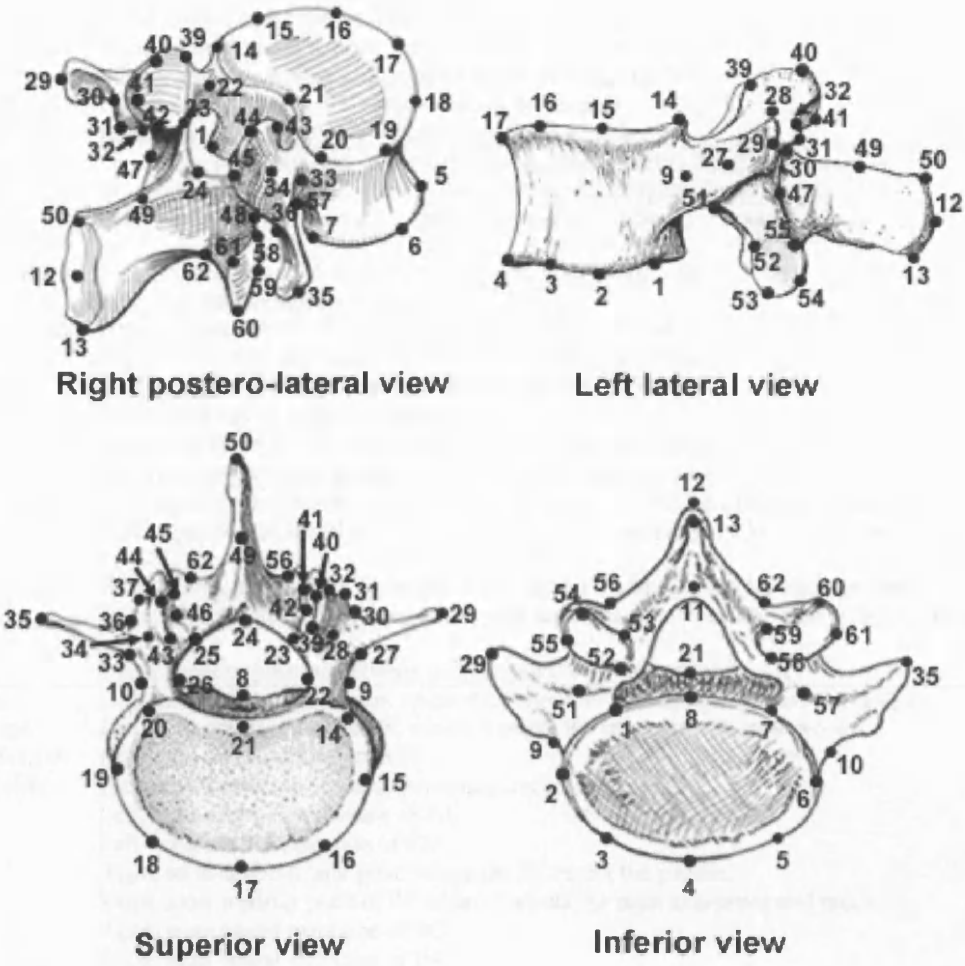


Figure 2.2 Location of 62 landmarks on a single lumbar vertebra. Right postero-lateral, left lateral, superior, and inferior views are shown. Modified from Kapandji (1992) and Platzer (1999), p.43, and redrawn after Aiello and Dean (1990), p. 283

Nr	Landmark	Description
1	Inferior surface of vertebral body; shape of pedicles	Left, inferior rim *Corpus vertebra* (CV), point where it meets with the pedicle
2		Left, most lateral point on inferior rim CV
3		Left, inferior rim CV, point mid-distance between 2 and 4
4		Inferior rim CV, most anterior point on the mid-sagittal line
5		Right, inferior rim CV point mid-distance between 4 and 6
6		Right, most lateral point on inferior rim CV
7		Right, inferior rim CV, point where it meets with the pedicle
8		Inferior rim CV, most posterior point on the mid-sagittal line
9		Left, point mid-length CV where it meets the pedicle
10		Right, point mid-length CV where it meets the pedicle
11	*Lamina* and inferior aspects spinous process,	Point on mid-sagittal line, where the inferior *Lamina* meets the spinous process
12		Point on mid-sagittal line, most posterior extension of spinous process
13		Point of mid-sagittal line, most inferior extension of spinous process
14	superior surface of vertebral body; and shape of pedicles	Left, superior rim, CV, point where it meets with the pedicle
15		Left, most lateral point on superior rim CV
16		Left, superior rim CV, point mid-distance between 15 and 17
17		Superior rim CV, most anterior point on the mid-sagittal line
18		Right, superior rim CV, point mid-distance between 17 and 19
19		Right, most lateral point on superior rim CV
20		Right, superior rim, CV, point where it meets with the pedicle
21		Superior rim CV, most posterior point on the mid-sagittal line
22	Vertebral canal	Left, superior junction between pedicle and CV on the rim of the *Canalis vertebralis* (CaV)
23		Left, superior junction of the *Lamina* with the left zygapophyseal joint facet, on the rim of the CaV
24		Point on mid-sagittal line where the rim of the CaV and the superior *Lamina* meet
25		Right, superior junction of the *Lamina* with the right zygapophyseal joint facet, on the rim of the CaV
26		Right, superior junction between pedicle and CV on the rim of the CaV
27	*Processus costales* and *accessorius*, left and right side	Left, most antero-lateral point where the *Processus costales* (PC) meets the pedicle
28		Left, most superior point of PC where it meets the left zygapophyseal process
29		Left, most lateral extension of PC
30		Left, most lateral extension of *Processus accessorius* (PA)
31		Left, most posterior extension of PA
32		Left, most medial extension of PA
33		Right, most antero-lateral point where the PC meets the pedicle
34		Right, most superior point of PC where it meets the right zygapophyseal process
35		Right, most lateral extension of PC
36		Right, most lateral extension of PA
37		Right, most posterior extension of PA
38		Right, most medial extension of PA
39	Zygapophyseal joint facets and superior zygapophyseal processes, left and right	Left, most superior-anterior extension of the *Facies articularis superior* (FAS)
40		Left, most superior-posterior extension of the FAS
41		Left, most inferior-posterior extension of the FAS
42		Left, point where the *Processus articularis superior* meets with the superior *Lamina*
43		Right, most superior-anterior extension of the FAS
44		Right, most superior-posterior extension of the FAS
45		Right, most inferior-posterior extension of the FAS
46		Right, point where the *Processus articularis superior* meets with the superior *Lamina*
47	*Lamina;* superior aspect of the spinous process	Left, most lateral laminar extension
48		Right, most lateral laminar extension
49		Spinous process, point on mid-sagittal line, mid-distance between 24 and 50
50		Spinous process, most superior-posterior extension, on mid-sagittal line
51	Zygapophyseal joint facets and inferior zygapophyseal processes, left and right	Left, deepest point of the greater vertebral notch curvature
52		Left, most anterior-superior extension of the *Facies articularis inferior* (FAI)
53		Left, most anterior-inferior extension of the FAI
54		Left, most posterior-inferior extension of the FAI
55		Left, most posterior-superior extension of the FAI
56		Left, point where the *Processus articularis inferior* meets with the *Lamina*
57		Right, deepest point of the greater vertebral notch curvature
58		Right, most anterior-superior extension of the FAI
59		Right, most anterior-inferior extension of the FAI
60		Right, most posterior-inferior extension of the FAI
61		Right, most posterior-superior extension of the FAI
62		Right, point where the *Processus articularis inferior* meets with the *Lamina*

Table 2.6 Definition of landmarks employed and sampled in the present study

For the set of 62 landmarks, wireframe and polygon representations were constructed using lines and triangles between landmarks to enhance the visualization of the vertebral shapes. Figures 2.3 and 2.4 illustrate the wireframe model as well as the transition from landmark sets to surface representation via polygons as computed by the software suite *morphologika*©.

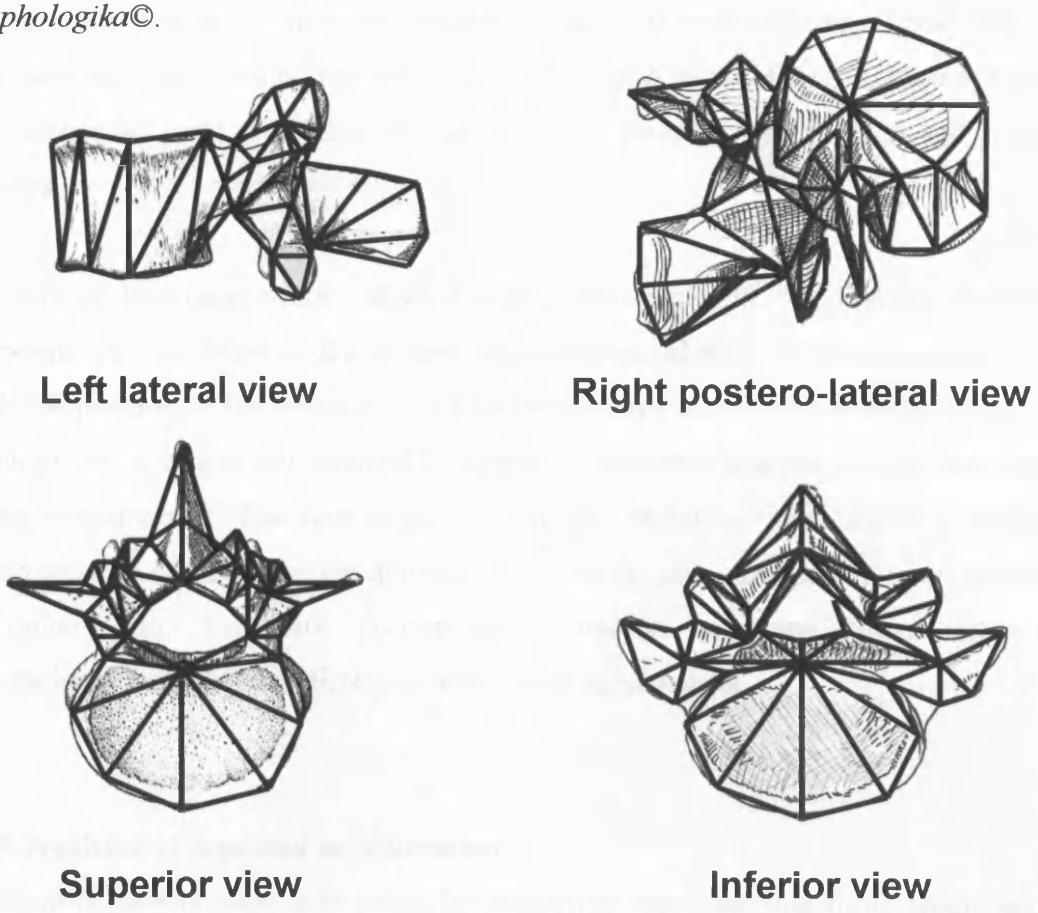


Figure 2.3 Wireframe models used to represent surface of the vertebral shapes. Different views are presented to facilitate visualization. Modified from Kapandji (1992) and Platzer (1999), p. 43, and redrawn after Aiello and Dean (1990), p. 283

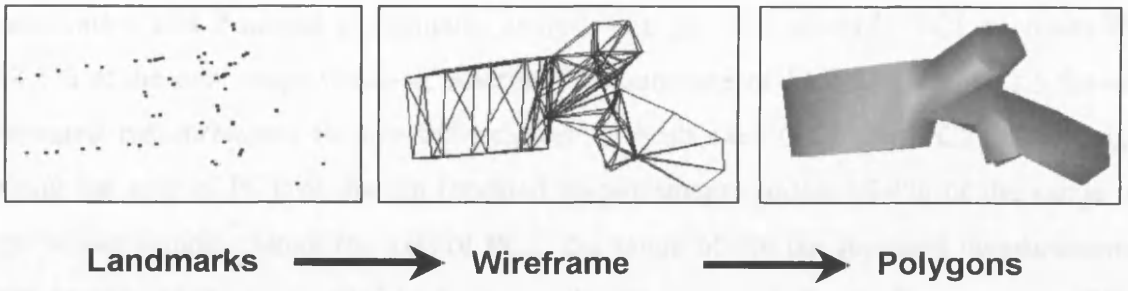


Figure 2.4 Visualization of landmark configurations. Transformation from landmark configuration to surface rendered object (polygon set) via wireframe as performed by the software suite *morphologika*©

2.3.4 Data collection

The adult specimens usually did not require special preparation before measurement. In the case of young infant specimens (humans and great apes) where the vertebral arch and body were not yet fused, the two parts were put together with white tack. This is stickier than blue tack but easily removed from bone material with water. The white tack used was produced by the technical staff of the Natural History Museum, London. The connected parts were then measured in the same way as a fused and complete vertebra.

The sets of landmarks were collected with a MicroScribe® G2 digitizer (Immersion Corporation). The MicroScribe consists of a mechanical arm, containing sensors which track the position of the stylus tip. The vertebrae were attached to a stand using a vice, which in return was firmly clamped to a table to guarantee that no motion was possible during measurement. The vices used to clamp the vertebrae were thickly padded with cotton wool in order to prevent damage to the bones, since the grip of the clamp had to be rather firm. Landmark co-ordinates collected with the MicroScribe were automatically recorded and displayed in an Excel spread sheet.

2.3.5 Precision of repeated measurement

Precision of measurement was tested by measuring one dissecting room specimen from the human material collection of the University College London (UCL R91, a 3rd lumbar vertebra) ten times. These repeated measurements were combined with the 47 measurements of the 3rd lumbars of the adult human sample. The combined sample was then Procrustes registered and PCA was performed on the GPA registered data. A plot of PC1 vs. PC2 is presented in figure 2.5 (for details about general Procrustes registration and Principal components analysis see pp. 124 onward). PC1 accounts for 19.3% of the total shape variance, whereas PC2 summarizes 11.7%. In figure 2.5 the ten repeated measurements form a tight cluster on both axes (PC1 and PC2). The range along the axis of PC1 of the ten repeated measurements equals 10.4% of the range of the whole sample. Along the axis of PC2, the range of the ten repeated measurements equals 15% of the range of the whole sample. The same applies to the remaining PCs. The scatter of the ten repeats is far smaller than that of the total human sample. Thus, in the case of humans (and most likely all other taxa in this study) errors due to

measurements are small compared to intra-specific variation and are therefore unlikely to influence the results.

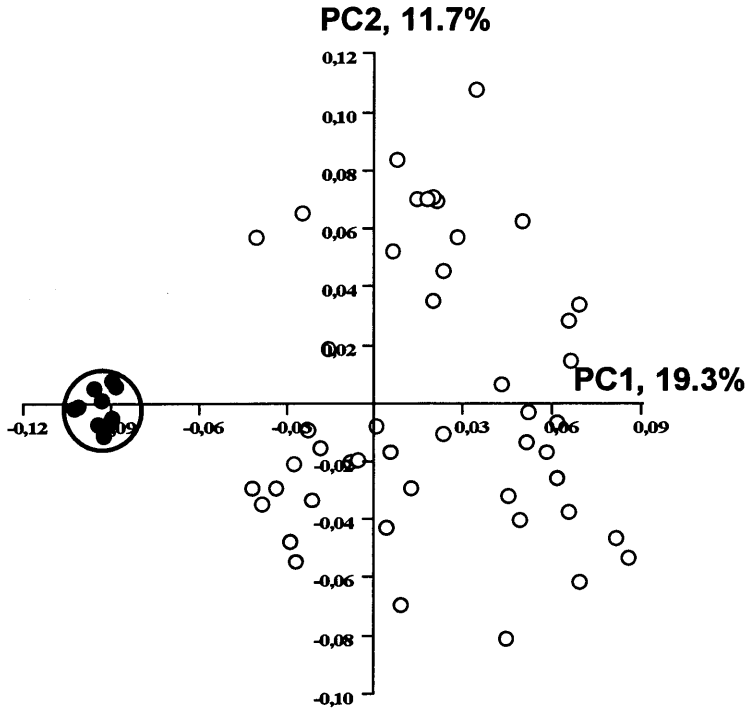


Figure 2.5 Scatter plot of PC1 vs. PC2 of adult human L3 sample with the addition of 10 repeats of measurement from L3, *H. sapiens* UCL R91, (a dissecting room specimen a contemporary male of Indian descent). ○ = male humans, O = female humans, ● = UCL R91

2.3.6 Taking measurements from CT-scans and three-dimensionally reconstructed vertebral representations

The original *A. africanus* Sts14 lumbar vertebral fossils are very brittle. Therefore, it is impossible to get permission to fix the bones in secure positions with clamps. This renders the task of collecting landmark data from these particular fossils very difficult. However, a cast of the last lumbar vertebra, Sts14a, has been produced by the Wenner Gren Foundation. Unfortunately, to date, this it is the only available cast for this particular lumbar vertebral series (correspondence with Janet Monge, the Casting Program at the University of Pennsylvania). Landmark data was collected from this cast. Nevertheless, the lumbar vertebrae of *A. africanus* Sts14 have recently been scanned with computer tomography technology at the Medical School of the University of the Witwatersrand, Johannesburg, South Africa. In this study, these CT scans were utilized to produce three-dimensional reconstructions of the vertebrae, using registration

and alignment tools from the software package amira™ (see figure 2.6). Figure 2.6 shows such a three-dimensional reconstruction of a lumbar vertebra of Sts14 (Sts14a, the last lumbar).

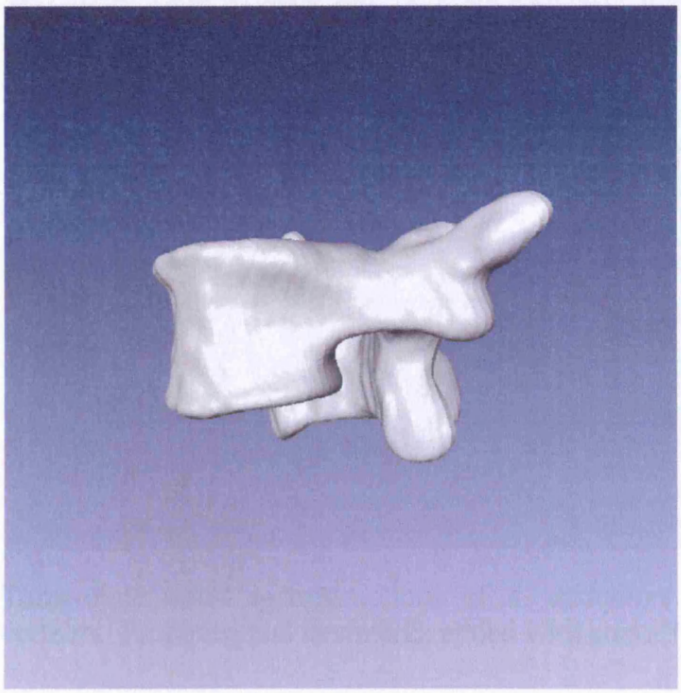


Figure 2.6 Three-dimensional surface reconstructions of *A. africanus* Sts14a, last lumbar vertebra. The surface rendering includes reconstructive materials added to the original vertebra by J.T. Robinson. Produced with amira™, left antero-lateral view

With the software amira™ it is possible to take landmark co-ordinates directly from the three-dimensional reconstructions of the vertebrae (see figure 2.7). Figure 2.7 shows the last lumbar vertebra Sts14a with the 62 landmarks positioned on the three-dimensional reconstruction.

The vertebral bodies of the third and fourth lumbar vertebrae (Sts14c and Sts14b) are extensively damaged (Robinson, 1972). These vertebral bodies as well as the costal processes were therefore reconstructed using tools provided by amira™.

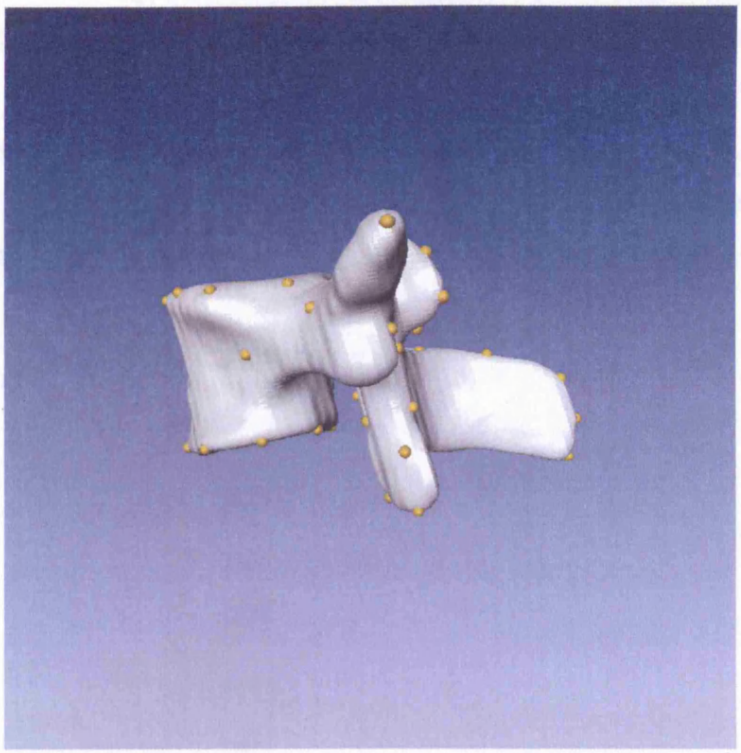


Figure 2.7 Three-dimensional reconstructions of *A. africanus* Sts14a, last lumbar vertebra. Produced and landmarks added with amira™, left lateral view

Since taking sets of three-dimensionally distributed landmarks directly from CT scan reconstructions is a novel technique, assessment of accuracy was called for. Further, it had to be checked if measurements taken with the MicroScribe can be compared with the ones taken from the CT scan reconstruction, which in principle should be possible.

The measurements taken from the available cast of Sts14a (fifth lumbar vertebra) were therefore compared with the ones taken from the three-dimensional reconstruction collected with amira™.

Figure 2.8 shows a plot of PC1 vs. PC2 of the GPA/PCA analysed landmark data (for details about GPA and PCA see pp. 124 onward) of the full sample of landmark configurations of *A. africanus*, Sts14. PC1 which represents 61.8% of the total shape variation (tsv), summarises shape differences between different lumbar vertebrae (L1, L2, etc). Along the axis of PC2, L3 shape data (both CT measurements) is separated from the rest of the sample. This is highly likely due to the fragmentary character of the vertebral body of this vertebra. Nevertheless, figure 2.8 shows that vertebral measurements taken with the MicroScribe and the ones taken with amira™ of L5

(Sts14a) cluster close together. Therefore, the measurements taken with amira™ were considered sufficiently similar to the ones taken with the MicroScribe and comparisons, including data collected by both methods, should not cause problems. In addition, the differences between two sets of measurements taken from the CT scan shape reconstruction are considered to be quite small. The second data set gathered from the CT data reconstructions lacks data for L2 (Sts14d) due to measurement mistakes.

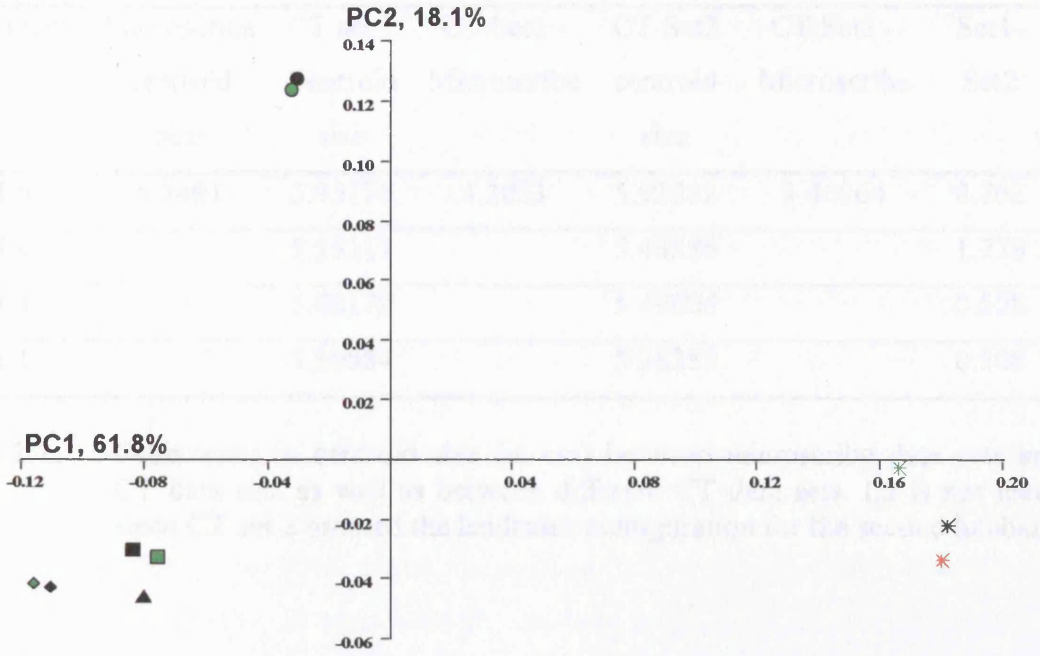


Figure 2.8 Scatter plot of PC1 vs. PC2 from full sample of *A. africanus* Sts14 landmark configurations (CT scan surface reconstructions and MicroScribe). MicroScribe collected landmarks from cast of L5 in **red**, landmark set 1 collected with amira™ in **black**, landmark set 2collected with amira™ in **green**. Set 2 is missing landmark configuration for second lumbar (2). ♦ = L1, ▲ = L2, ● =L3, ■ = L4, * = L5

To further assess differences between CT and microscribe data, the differences in centroid size between landmark configurations obtained from the last lumbar vertebra using each approach have been calculated. The comparison of the centroid sizes is shown in table 2.7. Differences in centroid size between the microscribe and CT data sets are less than 5 millimetres (= 3%) of the centroid size estimated from Microscribe data. This probably reflects errors in the production of casts, reconstructions and the difficulties in accurately locating landmarks in CT. Where two sets of CT data were available the mean was used predominantly in the analyses to minimise the effects of these sources of error. Table 2.7 also contains a comparison of centroid size between the

two CT data sets. Here, the error is much less (between 0.5 and 1.2% of mean CT centroid size). The largest difference is observed at the level of L4 and most likely caused by the reconstruction of the vertebral body of L4. The reconstruction made it possible to include the vertebra in the *A. africanus* sample but measuring data points in the reconstructed area was difficult. Nevertheless, differences do not exceed differences between CT data and microscribe data.

Vertebra	Microscribe centroid size	CT set 1 Centroid size	CT Set1 - Microscribe	CT Set2 centroid size	CT Set2 - Microscribe	Set1-Set2
L5	5.7891	5.95770	4.2823	5.92582	3.46964	0.762
L4		5.55117		5.48286		1.778
L3		5.48172		5.49806		0.508
L1		5.36684		5.38259		0.508

Table 2.7 Differences in centroid size (in cm) between microscribe data sets and CT data sets as well as between different CT data sets. L2 is not listed since CT set 2 omitted the landmark configuration for the second lumbar

2.3.7 The issue of comparing primate taxa with different numbers of lumbar vertebrae

How to compare the lumbar spine of primate taxa, when the number of lumbar vertebrae varies not only between but also within a species, is a problem that has always challenged researchers conducting comparative anatomical studies of the primate vertebral column. Since there is no one correct solution to this problem, ways around it usually depend on the particular questions a study addresses. One frequently utilized approach consists of selecting only one or two single (usually functionally relevant) vertebrae. From the results of their analysis, predictions applicable for the whole lumbar spine are then extrapolated. This approach was e.g. used by Shapiro (1993a) and Rose (1975). Another possibility as employed by Ward (1993b) consists of examining the variation of an anatomical feature, e.g. length of vertebral body, along the lumbar spine regardless of the total number of lumbar vertebrae in each taxon. Other authors defined vertebral levels along the lumbar spine which allowed the comparison of either functionally or phylogenetic equivalent vertebrae as seen by Sanders (1998), Sanders

and Bodenbender (1994), and Martelli and Schmid (2003). This latter approach is employed in the present study. This allows us not only to compare functionally (predominantly weight transmission) but also phylogenetically equal vertebrae. Five comparison levels were defined along the lumbar spine.

Based on studies of vertebral numbers by Schultz (1961), Schultz and Straus (1945), Häusler et al. (2002), and Pilbeam (2004), the most common patterns of distribution of thoracic and lumbar vertebrae in humans and the two most common patterns of African great apes are illustrated in figure 2.9. Although figure 2.9 illustrates the situation in modern humans and African great apes, some explanation about the pattern of vertebral inter-segmental distribution in *Pongo* is necessary. *Pongo* on average possesses only 23 instead of the 24 presacral vertebrae characteristic of Humans and African apes (Benade, 1990; Schultz and Straus, 1945). This is because, usually, there are only twelve thoracic vertebrae – as in modern humans, the last vertebra (#24) being part of the sacrum. Therefore, *Pongo* lumbar vertebrae are not phylogenetically equivalent with the ones of African great apes: *Pongo* L1 to L4 are actually homologous with African ape T13 to L3. Yet functionally they can be aligned very well with the lumbar vertebrae of African ape specimens with four lumbars. In order to facilitate the level-wise comparison of single lumbar vertebrae and because there are only twelve adult Pongo specimens in the sample, it was decided that the *Pongo* specimens be treated like African ape specimens with four lumbars, preserving functional equivalence at the expense of developmental homology.

Figure 2.9 shows the most common (Schultz, 1961; Schultz and Straus, 1945) distribution of vertebral morphology for presacral vertebrae 20 to 25 (counted from the atlas) in humans and African great apes (*Pan* and *Gorilla*). Various other patterns of vertebral regional variation for vertebrae 20 to 25 exist – especially in African apes (Pilbeam, 2004; Schultz, 1961; Schultz and Straus, 1945). However- with the exception of four chimpanzees from a population from the Ivory Coast, which all had only two lumbars – all African ape specimens show one of the two distribution patterns shown in Figure 2.11. For the purposes of analysis, therefore, 'vertebral comparison levels' were defined based on these three patterns.

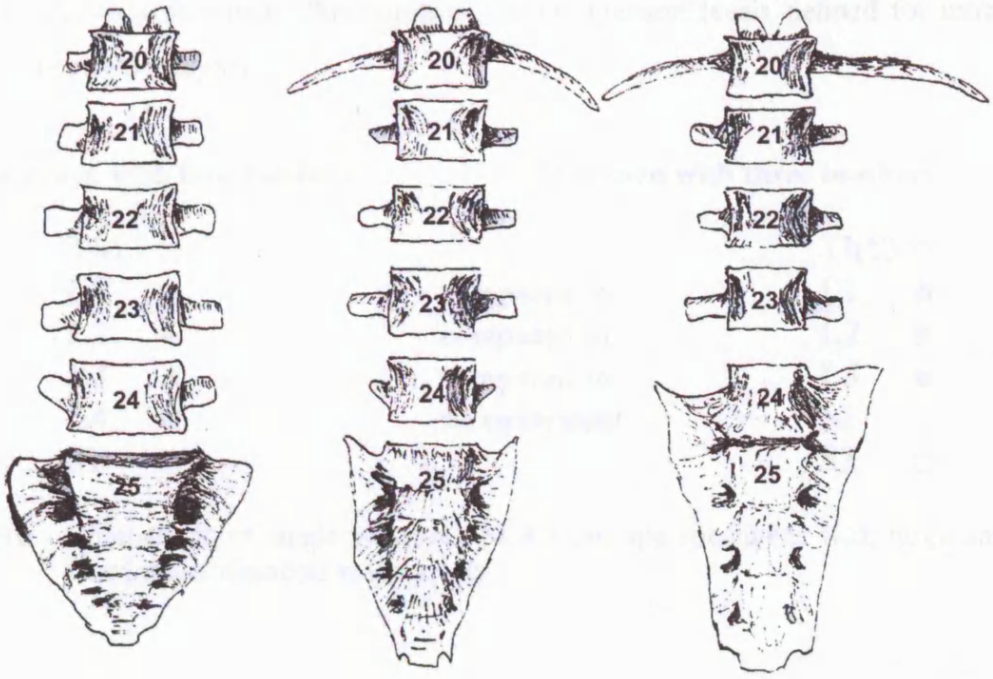


Figure 2.9 Distribution of thoracic, lumbar and sacral vertebrae in humans and African apes. Vertebral labels derive from counting from the atlas (C1) towards the sacrum

2.3.8 Defining 'vertebral comparison levels' in intra-specific comparisons of African great apes

In the case of intra-specific comparisons *Gorilla* and *Pan* specimens with three and four lumbar vertebrae respectively are compared. In the African apes, the first three lumbars are phylogenetically equivalent since there are no differences in the number of thoracic vertebrae of specimens with three and four lumbars: both have thirteen thoracic vertebrae. L4 on the other hand, does not have an equivalently free lumbar vertebra in specimens with only three lumbar elements (see figures 2.9 and 2.10). Therefore, on the level comparing last lumbars (level 4) only last lumbars of individuals with four free lumbars contributed to the samples. Thus, the sample size of African apes is diminished by about 30% (*Gorilla* and *Pan*) at comparison level 4. Since sample sizes in total are large (57 adult *Gorilla gorilla* specimens and 42 *Pan troglodytes* specimens), samples consisting only of specimens with four elements are considered large enough to yield statistically significant results when L4 is compared intra-specifically or inter-specifically to modern humans with more lumbars. The intra-specific comparison of *Pongo* did not pose a problem: all *Pongo* specimens in the study had four lumbars.

Figure 2.10 shows a schematic illustration of the comparison levels defined for intra-specific comparative analyses.

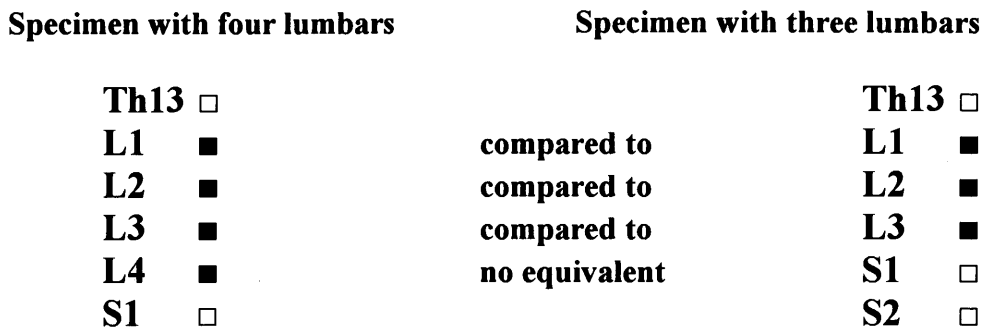


Figure 2.10 Comparison of single vertebrae of African ape specimens with three and four lumbar elements respectively

2.3.9 Defining 'vertebral comparison levels' in inter-specific comparative analyses between modern humans and all great ape taxa in the study

In inter-specific comparisons (humans, great apes) the variation in lumbar vertebral numbers is even greater in that humans have on average five lumbars and the great apes four or three. However, the same general approach as for the intra-specific comparison of apes with four and three lumbars is used, although with certain modifications.

According to figure 2.9, the first lumbar of humans is phylogenetically equivalent to the last thoracic vertebra of African great apes. Yet functionally, the first lumbars of humans and apes are more similar to each other since they both are "connecting" the lumbar spine with the thoracic one. To accommodate for both, the functional and phylogenetic differences of the position of the first lumbars of humans and African great apes, two vertebral comparison levels, named level 1, solution 1 and level 1, solution 2 are defined. Level 1, solution 1 acknowledges the functional equality of L1 of both modern humans and African apes. The first lumbars are compared regardless of their phylogenetic background.

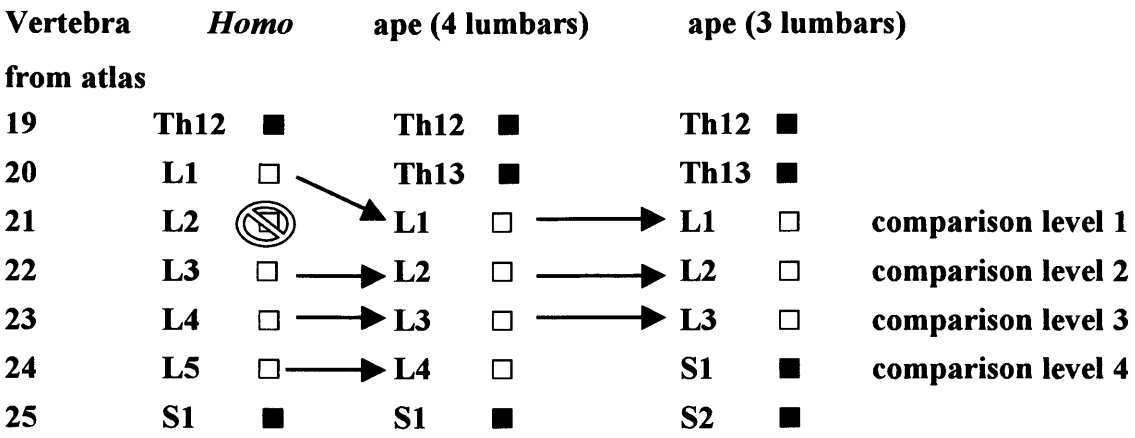


Figure 2.11 Inter-specific comparisons of single vertebrae, definition of levels of comparison with solution 1 for the first level of comparison. Arrows link the vertebrae that are compared with each other. Crossed out vertebral symbols are not included into the comparison

In level 1, solution 2, the second lumbar of humans is compared to the first lumbars of all ape taxa. In this, the phylogenetically equivalent vertebrae are compared. Ideally, no differences in results or only small ones will be recorded between level 1 solution 1 and level 1 solution 2. Figure 2.11 shows schematic illustrations of level 1 solution 1 and levels 2 to 4 whereas figure 2.12 illustrates the same for level 1, solution 2. Comparison levels 2 to 4 do not change from solution 1.

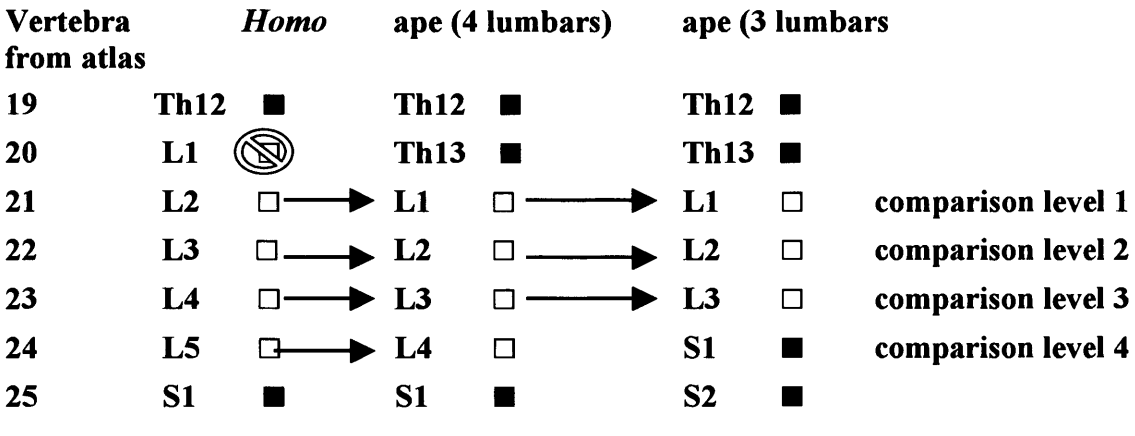


Figure 2.12 Inter-specific comparisons of single vertebrae, definition of levels of comparison with solution 2 for the first level of comparison. Arrows link the vertebrae that are compared with each other. Crossed out vertebral symbols are not included into the comparison

2.4 Analysis of landmark data

2.4.1 Geometric morphometric methods

The methods employed in this study to investigate lumbar vertebral morphology contrast with the ones predominantly used in previous studies e.g. (Benade, 1990; Martelli and Schmid, 2003; Odgers, 1933; Rose, 1975; Sanders, 1998; Schultz and Straus, 1945; Shapiro, 1993a) but for the application of geometric morphometric methods in the study of vertebrae see (Johnson et al., 1999; Johnson and O'Higgins, 1996; Johnson et al., 1989; O'Higgins, 1997; O'Higgins and Johnson, 1993; O'Higgins et al., 1989). Studies of the hominoid lumbar spine have relied on traditional approaches to the investigation of variation in morphology. In contrast to geometric morphometric methods these approaches are based on multivariate analyses of collections of inter-landmark distances, ratios and angles (Dryden and Mardia, 1998). These typically only represent part of the information that may be obtained from the position of the landmarks on which the measurements are based. The traditional methods do not take into account information about the spatial relationships among the measured variables (Rohlf, 1999). Intuitively, one expects methods that take the full 3-D information into account to have greater statistical power to detect differences in overall shape or co-variation with other variables (Rohlf, 1999). Another advantage of geometric morphometric methods is that the multivariate analysis of shape variables allows visualization of the actual shapes corresponding to points in the multivariate space of the analysis (Rohlf, 1999). The geometric morphometric approach provides a well understood statistical framework in which the variation of vertebral size and shape morphology can be investigated. Therefore, in this study, we employ geometric morphometric methods to access the high-dimensional complexity of the overall form of lumbar vertebrae and the lumbar spine as a whole.

2.4.2 Background

In biology, it is often the case that species compared to each other are relatively similar. D'Arcy Thompson, in 1917 considered deformations of form from one species to another in order to explain size-and-shape differences between them to be capable to account for the majority of differences observed between species. The ground breaking idea first brought forward by D'Arcy Thompson is that he worked with geometrical pictures of organisms rather than derived quantities (e.g. length of femur etc)

(Thompson, 1961). He suggested Cartesian transformation grids as a more analytical approach to the description of differences in form between e.g. species. He argues that recognizing in one form a definite permutation or deformation of another form lies within the immediate province of mathematics. Hence there is a powerful tool to quantitatively compare forms. D'Arcy Thompson also first introduced the idea of Cartesian transformation grids as a tool of visualization of shape differences in science (biology). In art, the concept has been frequently applied since the renaissance.

Although the power of Cartesian transformation in comparative morphology was recognized, its practical application to comparative morphology was not widely set in motion for several decades after the first publication of "*On Growth and Form*" (Thompson 1961). This was mainly because of the high complexity of the underlying mathematical operations when performed without the support of computers. In recent years, many key developments in shape analysis have been made which allow us to work with landmarks directly e.g. (Bookstein, 1991; Dryden and Mardia, 1998; Kendall, 1984; Mardia and Dryden, 1989; Mardia et al., 1979; O'Higgins, 2000; O'Higgins and Jones, 1998; Rohlf, 1999; Rohlf, 2000b). An intensive debate discussed the value of different (i.e. registration free vs. registration dependent) approaches to geometrics in the second half of the last decade e.g. (Bookstein, 1984; Lele, 1993; Lele and Richtsmeier, 1991; Mardia and Dryden, 1989). However, this was settled eventually by Rohlf (1999, 2000b) who confirmed concerns about statistical issues of registration independent approaches and showed superimposition/Procrustes distances (see later in this chapter) to be a stable, statistically powerful and well behaved approach to the analysis of landmark configurations. The advances made in technology used to measure/digitize landmarks are facilitating the use of geometric morphometric methods in numerous ongoing and recently published comparative morphological studies. In the following sections, the methods used in the present study will be introduced.

2.4.3 Superimposition

Geometric morphometric methods deal with Cartesian coordinate data representing landmarks chosen on the object of interest. The locations and orientations of landmark configuration differ between all shapes in a sample because they were different at the time they were collected. Further variation between landmark coordinates is observed due to differences in scale and shape. Therefore, before we are able to investigate

variations in shape within a sample of landmark configurations, the differences in location, orientation, and scaling have to be removed. The scale of landmark data is represented by centroid size. Centroid size is defined as the square root of the sum of squared Euclidean distances from each landmark to the centroid (the mean configuration calculated from the means for each landmark in the sample or the overall mean of the configuration of landmark coordinates) (Dryden and Mardia, 1998). Thus in the first step, the landmark coordinates are scaled to unit centroid size in relation to each other. Next, differences in location (translation) and orientation (rotation) between the landmark configurations are minimized, using least square techniques so that the sum of squared distances between them are as small as possible. This procedure is called Generalized Procrustes Analysis (GPA) (Dryden and Mardia, 1998).

2.4.4 How GPA and tangent projection works

Procrustes superimposition is a very useful tool for analysing landmark data. It can be used for estimating average shapes and for exploring the structure of shape variability in a data set. Also this method is very powerful in assessing distances between shapes. Procrustes analysis uses least square techniques to match landmark configurations through rotation, translation and scaling. It involves the least squares matching of configurations. Configurations are translated, rescaled and rotated relative to each other so that the total sum of square Euclidean distances between each and the mean is minimal. Once a sample of configurations has been iteratively matched into optimal full Procrustes position with respect to each other, the full Procrustes mean shape is calculated by taking the arithmetic means of each co-ordinate.

GPA produces estimates with the least error and no pattern of bias in comparison to alternative data adjusting methods (Rohlf, 1999; Rohlf, 2000b; Rohlf, 2003). GPA registration of data results in the representation of each shape (scaled, rotated, and translated) as a single point in a shape space. The shape space which results from GPA is described in detail by Kendall (1984). It is analogous to a sphere with unit diameter for triangles and hyper-sphere with unit diameter for shapes with more than three landmarks.

It is possible to use standard linear statistical methods despite the inherent curvilinearity of Kendall's shape space (Kent and Mardia, 2001) if variations are small (in relation to

Procrustes distances). This is because the projection from curvilinear (non-Euclidean) shape space into linearized tangent shape space will produce little distortion (Kent 1987). Nonetheless, Rohlf (1999) shows that statistical inference is not straightforward because for more than three landmarks, the resulting shape space is high dimensional and more complex. A practical way to circumvent this problem is to carry out PCA in a Euclidean tangent plane to Kendall's shape space (Dryden and Mardia, 1998). The projection of the original landmark configurations is represented as single points (plane coordinates) in the tangent plane, which correspond with the original sphere (shape space) coordinates. The point of tangency usually corresponds with a mean shape (reference shape) and its co-ordinates are referred to this origin (0/0/0) in the tangent plane, this is the approach used in this study. The coordinates in the tangent plane are used for subsequent statistical analyses. Shapes close to the reference shape will map to points close to the origin (0/0/0) (Rohlf, 1999). The projection of Procrustes tangent coordinates (projecting shapes from Kendall's shape space onto the Tangent plane) can be estimated with partial Procrustes tangent space projection (Dryden and Mardia, 1998; Rohlf, 1999; Rohlf, 2000b). Principal components analysis can be performed on tangent space (plane) coordinates, which extracts principal components of variation of shape (Dryden and Mardia, 1998).

2.4.5 Principal components analysis (PCA)

Principal components analysis (PCA) is a relatively simple multivariate statistical method. Based on combinations of presented variables, this analysis produces independent functions (components) which represent the total variability of a given sample (Manly, 1994). The components are ordered so that the first displays the largest amount of variation the second one displays the second largest amount and so forth. The aim of the analysis is to explain the maximum amount of variation within a sample with a minimum amount of components (Dryden and Mardia, 1998; Lamprecht, 1992; Manly, 1994). Therefore, some degree of economy is achieved and variation within the data is summarized and presentation is improved. The ability of PCA to summarise high dimensional distributions in lower dimensional spaces relies on the original variables being dependent on each other – the more the better.

Principal components analysis (PCA) is the most commonly employed multivariate method for exploring shape variability of landmark configurations after GPA and

tangent projection (Dryden and Mardia, 1998). A commonly used method (also employed in this study) is to perform PCA on the shape data. Hence each principal component (PC) summarizes a measure of some aspect of size or shape (Dryden and Mardia, 1998). PCA decomposes the total variability (the total sum of Procrustes distances) into orthogonal components with each PC successively explaining the highest variance in the samples of shape (Dryden and Mardia, 1998). Since PCA reduces data complexity, it is a very useful method for reducing the high dimensionality of the shape space. If there is a strong dependency between the chosen landmarks, only a few PCs may capture a large percentage of the variance. The scores of shapes on principal components (PCs) can be plotted to examine patterns of shape similarity and difference between landmark configurations after GPA. Likewise it is possible to work backwards from PC scores to shape and so to produce visualisations of the aspects of shape variability represented by PCs.

2.4.6 Thin-plate splines (TPS)

The qualitative and quantitative description of differences in size and shape between two or more objects is frequently of interest in biology. Measures such as Procrustes distances or values (percentages) of total shape variation attributable to PCs (from GPA/PCA) provide numerical measures for shape comparison yet they do not specifically indicate where the objects of interest differ nor are they informative with regard to the manner of differences.

Differences in shape can be visualized by computing the transformation of the space in which a given object lies into the space of a second object. This transformation will then provide the information about local and global shape differences between objects. Following the ideas of Thompson, a regular square grid pattern can be drawn on an object. This grid can then be deformed until it fits onto a second object, with corresponding parts (landmarks) located in the corresponding grid block. This technique provides useful visualization of local and global shape variation between objects.

Thin-plate splines (TPS) are a way of exploring this version of Cartesian transformation grids. Thin-plate splines are the most natural interpolant in two dimensions because they minimize the amount of bending in the transformation between two configurations. A regular square grid is drawn over the first figure (reference shape). Using the relative

locations of landmarks between the first (reference) figure, the grid is deformed to fit the second (target) such that landmarks map exactly and the space in between (and the gridlines) is smoothly deformed. In two dimensions this is achieved using a pair of thin plate splines transformations and in three dimensions three are used. A desirable property of splines is that they stay equivariant under location, rotation, and scale and are therefore registration free (Bookstein, 1989; Dryden and Mardia, 1998).

2.4.7 Procrustes distances as a measure of shape differences

In order to compare shape configurations, a measure of distance, in this case Procrustes distance, between them is employed. The Procrustes distance between one set of landmarks and the corresponding landmarks on another landmark configuration is defined as the minimum summed squared Euclidean distances between the landmarks of one landmark configuration and the corresponding landmarks of a second shape configuration (Bookstein, 1997; Dryden and Mardia, 1998). In the present study, this measure is frequently used to explore differences in shape intra-and inter-specifically and to estimate the level of significance of these differences in shape. In-house software (Viðarsdóttir et al., 2002) is employed to calculate the Procrustes distance between pairs of samples and simultaneously estimate levels of significance via permutation tests (see later in this chapter). The distances between mean shapes can also be visualized with the help of UPGMA phenograms (see later in this chapter).

2.4.8 Implementation of methods: The software suite *morphologika*©

The geometric morphometrics (GPA/PCA, thin-plate splines) used in the present study were all conducted using the software suite *morphologika*© (O'Higgins and Jones, 1998). *Morphologika*© provides a set of integrated tools for the examination and visualization of size and shape variation amongst objects represented by sets of landmark coordinates in two- and three-dimensions.

Morphologika© explores size and shape variation by first, registering (rotation, translation, and scaling) Cartesian coordinates from objects through GPA (as previously introduced). The data registration is followed by and examination of shape variation through PCA of tangent space coordinates. The software provides a display of graphical plots of the pairing of any two PCs or of any PC and centroid size. Shape variation is

visualized in terms of "morphings" of a three dimensional model of the mean shape. The mean shape can be presented as set of points (landmark configuration), wireframe model, or surface rendered object (polygon set) (see figure 2.4). Shape variation within the sample(s), displayed in the PC scatter plots can be investigated by "morphing" the mean shape along the axes of the PCs. Simultaneously, any warping of the mean landmark configuration can be viewed in the 3D viewer window. Figure 2.13 shows two screen captures of the *morphologika*© display window summarizing the various control boxes and viewers. Alternatively, shape variation can be visualized through the deformation of Cartesian transformation grids calculated using thin-plate splines (figure 2.13). All statistical and graphical output can be captured and integrated into standard software applications (e.g. Excel, SPSS; Microsoft Word or PowerPoint) for further (statistical) analysis or publication and presentation.

Morphologika© is distributed for free for non-profit use only. Further information on *morphologika*© can be attained from the authors directly or from the following web page: http://www.york.ac.uk/res/fme/resources/software.htm. To date, the software has been used successfully in a wide range of peer reviewed studies e.g. (Cobb and O'Higgins, 2004; Harcourt-Smith and Aiello, 2004; O'Higgins, 2000; O'Higgins and Jones, 1998)

2.5 Discriminant analysis

Discriminant analysis is used to determine which or which combination out of a group of variables discriminate best between two or more well defined groups (Kachigan, 1991; Manly, 1994; Statistica, 1984-2005). Or in other words: discriminant analysis tests how well it is possible to separate two or more groups of specimens given measurements for these specimens on several variables (predictor variables). Discriminant analysis is also used – based on a selected group of variables – to distinguish between different predefined groups and hence predict group membership of specimens of unknown origin (Field, 2000; Kachigan, 1991). Discriminant analysis is in some senses similar to multiple regression techniques. However, whereas in multiple regression analysis criterion variables are quantitative and data always consist of measurements of some kind, in discriminant analysis, memberships can also be predicted from criterion variables which are of a qualitative nature (e.g. coloration, presence/absence etc) (Kinnear and Gray, 2000; Manly, 1994).

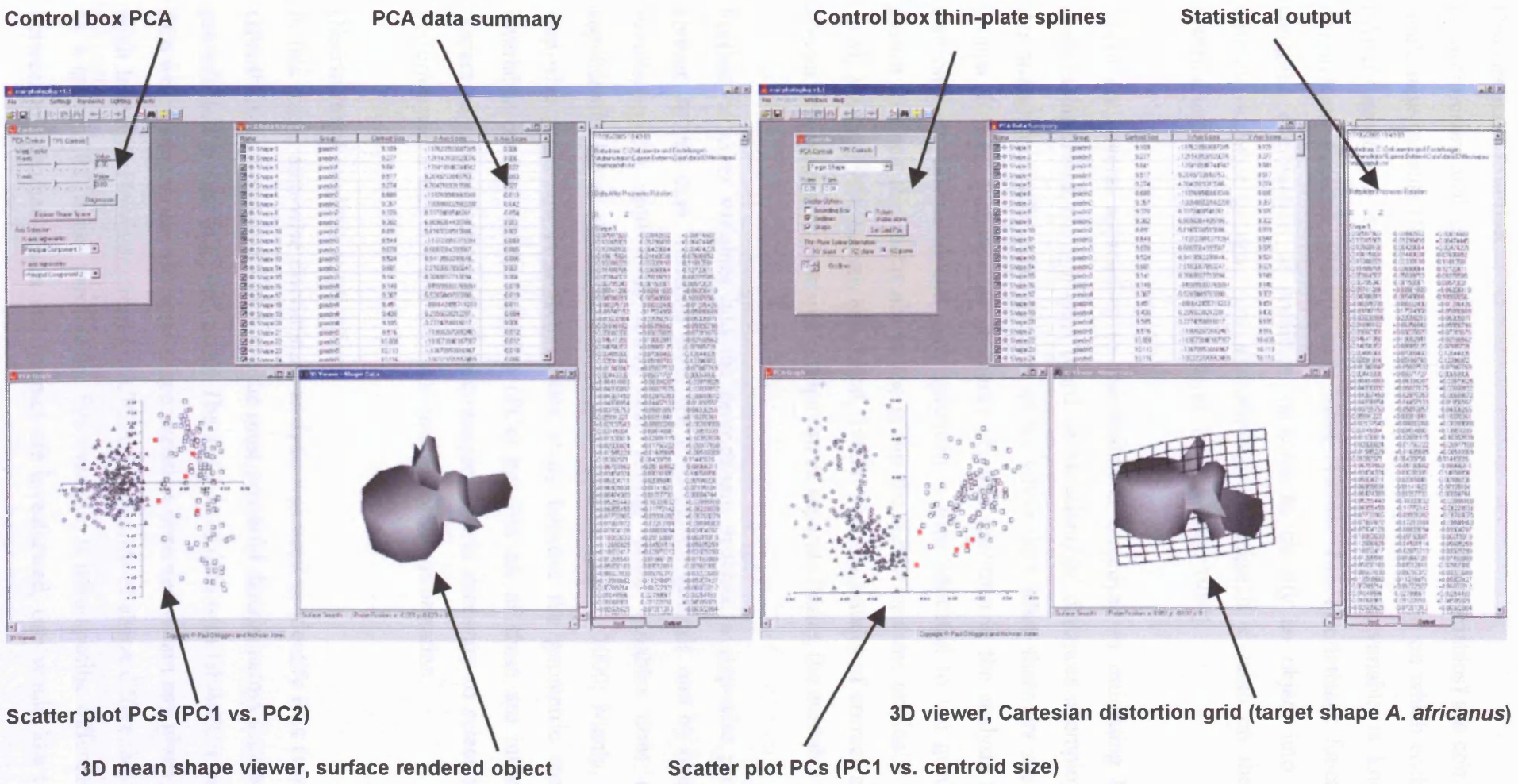


Figure 2.13 Two screen captures of *morphologika*© interface. Sample presented consists of *Gorilla gorilla, Pan troglodytes, Homo sapiens*, and A. *africanus*, n=335

Discriminant function

In discriminant analysis, predictor variables (independent variables) are combined into a single new variable (for two groups, more for more groups) on which each participant (object, specimen) in the study gets a score. This new variable is known as the discriminant function (Sneath and Sokal, 1973). The discriminant function uses a weighted combination of predictor variables to classify an object into one of the criterion variable groups – or alternatively, to assign it a value on the qualitative criterion variable (Field, 2000; Kachigan, 1991; Manly, 1994).

There are several approaches to discrimination employed in estimating likely group membership. Here, the approach based on Mahalanobis' distances is employed because this straightforwardly takes account of the whole data when there are more than two groups. Briefly, Mahalanobis' distances of each specimen in the analysis to all group centroids are calculated and each specimen is then allocated to the group that it is closest to albeit this might not be the group the specimen came originally from (Field, 2000; Manly, 1994; Sneath and Sokal, 1973). The percentage of correct allocations is also an indication as to how well groups can be separated using the available variables.

Further, to enter variables into the discriminant analysis, a step-wise procedure was chosen. In this case, variables enter the discriminant analysis one by one (instead of simultaneously) until it is found that adding extra variables does not provide significantly better discrimination between groups (Field, 2000; Manly, 1994). The step-wise procedure is chosen in this study because the geometric shape analyses invariably produce many variables (PCs) but not all of these are informative with respect to group discrimination. In consequence it is necessary to select a subset that performs well in this task and does not omit important information.

Discriminant analysis applications

In this study, step-wise discriminant analysis was used to identify PCs (variables) from GPA/PCA analysed data which are the most powerful discriminators separating variable pre-selected groups (e.g. sex, taxa). The analysis of data with GPA/PCA yields a set of PCs which summarizes the total shape variation observed within any given sample (e.g. adult humans). However, from GPA/PCA the *quality* of shape differences summarized by a specific PC is not predictable. For example, if intra-specific differences in shape between e.g. human males and females are investigated, one would like to be able to

identify the PCs that best separate the sexes. Once these PCs are identified, differences in shape summarized by them can be described as being most important in separating male from female humans (in this example).

2.5.1 Statistical significance and correlation tests

Measures such as Procrustes distances or values attributable to PC scores provide numerical measures for shape comparison. However, these measures do not provide information on the level of significance attributed to differences in shape between objects. Therefore, further statistical tests are necessary to estimate levels of significance of results from GPA/PCA of landmark data. In this study, several different tests of significance will be used according to the requirements a particular analysis provides.

Once the significance of differences in shape are confirmed, it is of further interest to explore how they are related to other variables, e.g. body size, locomotion, etc. Therefore, correlations between differences in shape and specific variables are tested. In the following sections, significance and correlation tests which have been most widely applied in the present study are introduced.

2.5.2 Permutation tests

Permutation tests are suitable for assessing the significance of shape differences because they do not utilise prior assumptions about equality of variance, distribution etc between the groups of specimens being compared. Permutation tests are robust methods that are not rendered invaluable by outliers and "broad tails" (Bookstein, 1997; Good, 1994). In the present study, permutation tests were performed using in-house software (Viðarsdóttir et al., 2002), designed to calculate the significance of Procrustes distances between two groups. 1000 iterations (permutations) were conducted in each test application. After calculating the Procrustes distances between two group means, individuals are randomly allocated to each group and the means are recalculated. The original distance is then compared to the distribution of the permuted distances. If the original Procrustes distance falls outside the 95% range of variation, it is considered to be significantly different with a $p<0.05$.

2.5.3 Independent T-tests

The T-test is the most commonly used method to evaluate the differences in means between two groups. Theoretically, the T-test can be used even if the sample sizes are very small (e.g., as small as 10), as long as the variables are normally distributed within each group and the variation of scores in the two groups is not reliably different (Manly, 1994). The p-level reported with a T-test represents the probability of error involved in accepting a research hypothesis about the existence of a difference. T-tests are limited to single variables such as the scores of groups on a particular PC or centroid size. In this study T-tests were performed using the analytical software SPSS (version 8.0 for PC) and were used to assess the significance of differences in vertebral size between sexes (within a taxon) and between taxa.

2.5.4 Pearson's correlation coefficient

Correlations between two variables are often assessed with Pearson's correlation coefficient. It determines the extent to which values of two variables are linearly related to each other. The value of the correlation coefficient represents the extent to which there exists a linear relationship between two variables. The significance level calculated for each correlation is a primary source of information about the reliability of the correlation. Due to standardizing the covariance, values for Pearson's correlation coefficient can have values between +1 (perfect positive correlation and -1 (perfect negative correlation). A coefficient of 0 indicates no linear relationship at all. If the correlation coefficient is squared, then the resulting value (r^2, the coefficient of determination) will represent the proportion of common variation in the two variables (i.e., the "strength" or "magnitude" of the relationship) (Field, 2000).

A problem arising in relation to linear correlation is that Pearson's correlation coefficient measures linear relationships between two variables only. Non-linear relationships will not give sensible results with regard to the association between variables. The examination for linearity of the scatter plots resulting from GPA/PCA is therefore a necessary step in evaluating correlations. The significance of a correlation coefficient of a particular magnitude will change depending on the size of the sample from which it was computed. Thus when sample sizes are small, significance levels have to be regarded with some caution.

In some cases in the present study, it was of particular interest to see if a relationship exists between vertebral size or shape and some variable (e.g. body weight). In these cases, Pearson's correlation coefficient was calculated. In the present study, Pearson's correlation coefficient was calculated using the analytical software SPSS (version 8.0 for PC). Results were accepted as significant if the p-values were < 0.05. They were considered highly significant if the p-value was < 0.01.

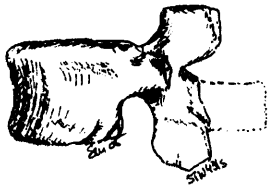
2.5.5 Bonferroni corrections

When multiple tests of significance are carried out some correction of the p-values is required due to inflated rates of "familywise" errors (Field, 2000). This is because an increased number of significance tests increases the risk of falsely rejecting the null hypothesis (type I error). The most straightforward correction is that of Bonferroni (Field, 2000). The familywise error of a particular set of multiple tests of significance is calculated as follows: $1-(0.95)^n$, which provides a measure of the chance of having made at least one type I error. Furthermore, to accept a p-value of 0.05 for significance of the differences overall, the adjusted p-value would be calculated as 0.05/n, where n is the number of significance tests and used as the criterion for judging significance. For example, in the case where four lumbars are compared between two taxa the Bonferroni test indicates that the there is a 18.5% chance of having made at least one type I error and the appropriate p-value required to accept any one test (between a pair of species at a particular level) is $0.05/4=0.0125$. The disadvantage of the Bonferroni correction is to be seen on the grounds that it is too conservative: each individual test is held to an unreasonably high standard. This increases the probability that legitimately significant results will fail to be detected (increased rate of type II errors). For this reason in subsequent analyses within this thesis the results of independent tests are given without correction but where the correction would affect the conclusions this is stated, leaving the reader to judge the validity of the raw and corrected results.

2.5.6 UPGMA phenograms

UPGMA stands for **u**nweighted **p**air-**g**roup **m**ethod using **a**rithmetic means (Sokal and Rohlf, 1981). The original purpose of this method was to construct taxonomic phenograms, which are tree-diagrams that reflect the phenotypic similarities between operational taxonomic units (OTUs) (Opperdoes, 1997). UPGMA is a simple method of

tree-diagram construction. It employs a sequential clustering algorithm, in which local topological relationships are identified in order of similarity, and a phylogenetic cluster diagram is built in a stepwise manner. In a first step, among all the OTUs the two OTUs that are most similar (distances) to each other are identified and then treated as a new single 'composite' OTU. Subsequently from among the new group of OTUs (composite and simple), the pair with the highest similarity is identified and clustered. This continues until only two OTUs are left. In this study, UPGMA phenograms are used only for visualisation of shape differences between mean shapes as represented by Procrustes mean distances. There is no attempt made here to display the phylogenetic relations e.g. between taxa. In this study, UPGMA phenograms were calculated using the program NT-SYS (© Exeter Software, 47 Route 25A, Suite 2, Setauket, NY 11733-2870, USA).



CHAPTER III INTRA-SPECIFIC VERTEBRAL SIZE AND SHAPE VARIATION

Patterns of intra-specific shape variation in the lumbar spine are different in modern hominoids (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus,* and *Homo sapiens*)

3.1 Introduction

This study examines intra-specific lumbar vertebral size and shape variation within the hominoid taxa *Homo sapiens, Gorilla gorilla, Pan troglodytes,* and *Pongo pygmaeus.* Sexual dimorphism is the major influence on intra-specific variations that will be investigated here. Body weight and locomotor repertoires (frequencies of locomotor modes and kinematics) differ between the sexes of many hominoids. It is therefore important to investigate the potential influence of these differences in weight on vertebral size and shape. Further, this study attempts to establish how intra-specific differences in size and shape develop within each species due to heterochronic processes throughout ontogeny.

The results from this study provide a framework for later studies of inter-specific variation of lumbar vertebral size and shape and for the analyses of fossil hominins in comparison to modern hominoid taxa (these studies are presented in Chapters IV and V). Future studies of fossil hominin vertebrae will benefit from knowledge of how and if differences in overall body weight and size might influence the size and shape of lumbar vertebrae. This is because there is evidence that some fossil hominin taxa were highly sexually dimorphic in overall body size e.g. (Häusler and Schmid, 1995; Lockwood et al., 1996; McHenry, 1991c; Richmond and Jungers, 1995; Wood and Richmond, 2000)

3.2 Background

In the following paragraphs, sexual dimorphism in body weight as well as in locomotor repertoires for each of the taxa in the study is reviewed. Living primates vary considerably in size and weight (Fleagle, 1976; Martin, 1990). Thus, much of the diversity observed in e.g. structure, physiology, behaviour, and ecology is related to

differences in body weight (Jungers, 1985a; Schmid-Nielsen, 1975). In sexually dimorphic taxa, it is of interest to investigate how males and females (of the same taxon) of different size maintain functional equivalence. Additionally presented are the pro and contra-arguments that intra-specific differences in locomotor repertoires have a relationship with intra-specific differences in vertebral size and shape.

3.2.1 Sexual dimorphism in great apes and humans

Sexual dimorphism should be considered when explaining variation observed in fossil hominin specimens. In the case of fossil hominin studies, this might be of importance. *A. afarensis* as well as *A. africanus* are considered highly sexually dimorphic taxa, e.g. (Lockwood and Tobias, 1999; McHenry, 1991b; McHenry, 1991c; Plavcan, 2003; Richmond and Jungers, 1995; Susman et al., 2001). Conversely, if sexual dimorphism can be ruled out (as a result of studies of extant relatively closely related groups) as the reason for shape variation within a fossil taxon, other hypotheses (e.g. locomotor function) can be explored to explain apparent differences in morphology.

Sexual dimorphism varies in hominoids. In *Gorilla* and *Pongo* sexual dimorphism is very evident in the differences in body size, body weight, muscular development, and size and shape of the cranium and canines between the sexes (Rowe, 1996; Sonntag, 1924) (for differences in body weight and ♂/♀ weight ratio see table 3.1). Additionally, the male *Pongo* face is adorned with very distinctive cheek pads (Nowak, 1999; Rowe, 1996), whereas dominant *Gorilla* males have a silver coloured back (Nowak, 1999; Rowe, 1996; Schaller, 1963). Male chimpanzees, on the other hand, are only moderately heavier than females and there is a big overlap in body weight between the sexes (Rowe, 1996). However, the most obvious sexual dimorphism observed in chimpanzees is the presence of sexual skin surrounding the external genitalia which changes colour and size dramatically (swelling) during the sexual cycle (Fleagle, 1999). Humans, finally, show differences in body size and body weight between the sexes which are slightly smaller than those observed in chimpanzees (see table 3.1). Differences in canine size are negligible and differences in skull morphology show considerable overlap between the sexes (Mace, 1992).

Sex	*Homo sapiens*	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*
Female	**55** ± 4.62 (1sd = 2.31)	**91.4** ± 23.6 (1sd = 11.8)	**38.1** ± 5.0 (1sd = 2.5)	**38.2** ± 3.0 (1sd = 1.5)
Male	**68** ± 15.5 (1sd = 7.75)	**177.8** ± 47.2 (1sd = 23.6)	**49.2** ± 9.8 (1sd = 4.9)	**75.7** ± 10.0 (1sd = 5.0)
♂/♀ **Weight ratio**	**1.2** **120%**	**1.95** **195%**	**1.3** **130%**	**2.0** **200%**

Table 3.1 Male and female hominoid body weights in kg. ♂/♀ weight ratio also shown in in %. Values are compiled from the following sources: Delgado and Van Schaik (2000), Jungers (1985a), MacKinnon (1974), McHenry (1992a,b), Novak (1999), Plavcan and Van Schaik (1997), Rowe (1996), and Ruff (1991)

3.2.2 Sexual dimorphism in the primate vertebral column

Studies concerning sexual dimorphism of trunk and spine morphology - the lumbar vertebrae in particular - are scarce in non-human primates as well as in humans. One available study by Taylor (1984) shows that from the age of eight years onwards, the dimensions of human thoraco-lumbar vertebral bodies are significantly sexually dimorphic. Female thoracic and lumbar vertebral bodies are relatively longer and have a relatively smaller medio-lateral diameter than male ones. Taylor observed that the differences in male and female vertebrae resulted from an early growth spurt in vertebral length in the female thoraco-lumbar spine. In addition, the male growth spurt occurs in the horizontal rather than cranio-caudal direction. Therefore, male vertebrae gain more in medio-lateral body width than in vertebral body length. According to Taylor, differences in the start and timing of female and male puberty are responsible for differences in growth patterns. Intra-specific differences in the degree of lumbar lordosis and wedge shape of the lumbar vertebral bodies have been repeatedly reported for modern humans (Cheng et al., 1998; Fernand and Fox, 1985; Grados et al., 1999; Shao et al., 2002). Results indicate that women have a larger lordotic angle which is a measurement of the magnitude of the lordotic curvature and there is also a significant correlation between vertebral body shape and the lumbar lordotic angle. Furthermore, female vertebrae are more posteriorly wedge shaped. Nevertheless, these two features, lordotic angle and posterior wedge shape of lumbar vertebral bodies, not only correlate strongly with sex but also with age (Amonoo-Kuofi, 1991; Shao et al., 2002).

In the case of sexual dimorphism in the primate postcranium, Schultz (1953) noted that

"Sex differences in the relative thickness of the limb bones favour males in all forms - ...- the difference being particularly marked in types with great sex differences in body size".

According to Schultz, these differences are also observed in the vertebral column although he did not link this with any specific vertebral elements (e.g. vertebral bodies, or vertebral processes). However, Schultz (1938) also reports that all male hominoids tend to have longer cervical and thoracic spinal regions and shorter lumbar ones than females.

3.2.3 Sexual dimorphism in hominoid locomotor repertoires

Over the last few decades evidence for sexual dimorphism in locomotor repertoires in great apes has been gathered in several field studies e.g. (Cant, 1987b; Doran, 1997; Isler, 2003; MacKinnon, 1974). A brief summary of these differences in presented here for each taxon.

Gorilla gorilla

Extensive studies of *Gorilla* in its natural habitat indicate the presence of intra-specific differences in locomotor repertoire of different *Gorilla* subspecies, namely *Gorilla gorilla gorilla* and *Gorilla gorilla beringei*). Generally, there are also inter-specific differences observed between the sub-species; lowland gorillas seem to be more arboreal or at least more seasonally arboreal than mountain gorillas (Remis, 1995). Intra-specific differences in locomotor repertoires within each sub-species consist mostly of the observation that males in general spend more time on the ground and less in trees. If the males spend time in trees, they stay closer to the core of the tree, engage less in thin branch climbing and display less suspensory climbing behaviour than the females (Remis, 1995; Remis, 1999). Remis (1995) argues that the larger body size and weight of male *Gorilla* enables them to monopolize the easily accessible food resources on the ground, or close to the core of trees. Support for this hypothesis is seen in that females stay more on the ground and close to the tree core if the males are away. In addition, differences in substrate use and hence locomotor repertoire in relation to body weight have been reported for different age groups: gorillas spend successively less time

in trees or their periphery respectively and more on the ground, the older they become (Isler, 2003). They also engage in less suspensory climbing behaviour the older they become (Doran, 1997; Isler, 2005).

Pan

Studies of *Pan* yield similar results as observed in *Gorilla.* Intra-specific differences as well as inter-specific differences between sub-species are observed in the respective locomotor repertoires. Sexual dimorphism in body weight and locomotor repertoire between the two chimpanzee species *Pan troglodytes* and *Pan paniscus* have been a focus of research. *Pan paniscus* is the more arboreal species (Doran, 1993 b). Additionally, male bonobos engage more in suspensory climbing behaviour than male common chimpanzees. Within *Pan troglodytes*, it has been noted that males are generally less arboreal than females but, if engaged in arboreal locomotion, males employ more different types of locomotor modes (climbing, scrambling, and bipedalism) and less arboreal quadrupedalism than females (Doran, 1993a). As in gorillas, juveniles are observed to climb more frequently than adults (Doran, 1997; Isler, 2005; Pontzer and Wrangham, 2004). The further in their postnatal development towards adulthood, gaits of great apes become more energetically efficient (Pontzer and Wrangham, 2004).

Pongo pygmaeus

Among the great apes, *Pongo* is the most arboreal taxon. Both sexes have a varied arboreal locomotor repertoire which consists of clambering, vertical climbing, brachiation, tree-swaying, and quadrupedal climbing (Cant, 1987a; Cant, 1987b; Hunt, 1991b; MacKinnon, 1974). Intra-specifically, it has been reported that male *Pongo* use larger substrates, closer to the core of trees than females and that they use more supported positions (sitting, bipedal standing, tripedal standing) than females, which are more often engaged in suspended postures (hand-foot hanging, one hand hanging) (Cant, 1987a). Furthermore, it has been observed that on Borneo, males and females engage in equal amounts of tree-swaying whereas on Sumatra, males engage in this locomotor mode far more often than females. On Borneo, males sometimes travel between trees on the ground whereas females rarely leave the canopy and the understorey levels of trees. On Sumatra on the other hand, both taxa hardly ever come to the ground, probably due to larger predator pressure caused by the presence of Sumatran tigers (Cant, 1987b).

Studies investigating differences in locomotor repertoire between sub-adult and adult orang-utans are very scarce. However, the few studies that are available, show that, in contrast to African great apes, in *Pongo*, sub-adult and adult individuals do not differ in the time spent in the forest canopy (Cant, 1987b; Thorpe and Crompton, 2005). According to Isler (2005), juvenile *Pongo* individuals climb vertically more frequently than adult individuals and with a higher limb cycle frequency which also was more symmetric than in adults (Isler and Thorpe, 2003). In general, the juveniles show a reduced range in joint motion. These intra-specific differences in vertical climbing locomotion between sub-adults and adults is seen in relation to differences in body size and weight between the adults and sub-adults (Isler, 2005).

Homo sapiens

Both sexes in *Homo sapiens* engage exclusively in habitual bipedalism as the main locomotor repertoire. Two different modes of bipedal locomotion are discerned: walking and running. Walking resembles an inverted pendulum motion and one foot always has contact with the ground (Alexander, 1992). First contact of the foot with the ground consists of heel strike, followed by toe off. The leg is fully extended. In running, on the other hand, there is an airborne phase (both feet off the ground). First contact of the foot with the ground consists of a mid plane touch down and legs are usually bent at hips and knees during running (Alexander, 1992). From these short summaries of running and walking, it is clear that the two locomotor modes require different adaptations in the postcranium. Humans are not particularly good sprint runners but excellent endurance runners at relatively high speeds. No differences have been reported so far in either running or walking frequencies between males and females.

3.2.4 Sexual dimorphism in hominoid locomotor kinematics

In contrast to studies of sexual dimorphism in locomotor repertoires, there is less known about sexual dimorphism in great ape locomotor kinematics. However, recent studies of kinematics of vertical climbing in hominoids indicate some differences between the sexes in *Gorilla*, but not *Pan* and *Pongo* (Isler, 2005; Isler and Thorpe, 2003; Thorpe et al., 1999). Differences in locomotor kinematics between male and female gorillas consist of shorter stride length (relative to leg length) and reduced limb joint motion observed in the male. Compared to great apes, modern humans show considerable

sexual dimorphism in locomotor kinematics. In contrast to sexual dimorphism in locomotor repertoires, there are important biomechanical differences in the bipedal gait of men and women. For example, Li et al. (1996) and Oberberg et al. (1993, 1994) found differences between the sexes in gait parameters such as step length and gait speed but not in step frequency. Even more interesting (for the present study), Schache et al. (2003) report significant differences in the angular rotation of the lumbo-pelvic–hip complex between men and women during walking. These results are highly likely related to the well known sexual dimorphism in pelvic morphology which evolved due to obstetric necessities (Häusler and Schmid, 1995; Ruff, 1996; Schultz, 1949).

3.2.5 Why are hominoid locomotor repertoires intra-specifically different?

In summary, field observations have shown that adult females of both *Gorilla* and *Pan* are more arboreal than adult males. There may be several reasons for these observations. Males, at least in *Gorilla* are considerably heavier than females, thus they are less inclined to use small branches or to engage in suspensory arboreal behaviour than smaller individuals (namely females and juvenile specimens). Furthermore, due to their large body size, *Gorilla* males can monopolize easily accessible food resources on the ground as well as in the trees (close to the tree core) (Remis, 1999). In chimpanzees, the body weight argument is less convincing since body size dimorphism in *Pan* is small. However, social structures might allow male chimpanzees to monopolize the easily accessible terrestrial and arboreal food resources (Remis, 1999).

In the Asian great apes, both sexes are almost exclusively arboreal. Nevertheless, males are observed more often travelling on the ground and more so on Borneo than on Sumatra where predatory pressure through tigers is present (Cant, 1987b). Since males (at least the fully matured specimens) weight far more than females, it might sometimes be more difficult for them to move from one tree to another the canopy than for the lighter females, hence the higher frequency of terrestrial locomotion in the former (Cant, 1987a; Cant, 1987b).

3.2.6 How does sexual dimorphism develop in primate postnatal ontogeny?

The present study is not a growth study. There are no longitudinal data available on individuals growing from infant to adulthood which would allow us to study in detail

how vertebral size and shape develop within an individual. However, an attempt will be made here to see if it is possible to identify the patterns of postnatal ontogeny that lead to sexual dimorphism in lumbar vertebral size and shape in some of the hominoid taxa in this study.

There is not much data on how postcranial sexual dimorphism develops postnatally in primates. The studies that investigate the development of hominoid sexual dimorphism, concentrate primarily on the skull and the canines where sexual dimorphism is most evident (Ashton, 1956; Ashton and Zuckerman, 1950; Cobb and O'Higgins, 2004; Plavcan, 2001; Plavcan and Van Schaik, 1997). In general, if intra-specific differences in vertebral size and shape develop early in ontogeny, it is highly likely that their development is under tight genetic control and hence related to phylogeny. However, if intra-specific differences in vertebral size and shape appear at later stages in ontogeny, they may have a close relationship with scaling and function (i.e. increase in body weight).

Sexual dimorphism in adult specimens might arise through some combination of the following. 1) Differences in vertebral size and shape might already be established prenatally and are carried to adulthood. 2) They might arise through intra-specific differences in size and shape trajectories. And 3), ontogenetic size and shape variation trajectories might differ in duration that is the degree of postnatal size and shape variation between males and females. This latter scenario can be achieved in two ways or a combination thereof: the same size or shape trajectory can vary between sexes in time. This means one sex has an extended growth period or one sex has a stipulated one. Alternatively, intra-specific differences in adult size and shape can be achieved following the same trajectories but with different growth rates (hypermorphosis). Often, a combination of differences in time and growth rate is present (de Leon and Zollikofer, 2001; Mitteroecker et al., 2004).

3.3 What is new in this study?

In this study, the intra-specific differences in size and shape of the lumbar spine within four hominoid taxa will be investigated and discussed in relation to sexual dimorphism and weight transmission function through the lumbar spine.

Further, this study investigates when and how intra-specific differences in lumbar vertebral size and shape, observed in adult specimens, are established in postnatal ontogeny. Is sexual dimorphism in vertebral size and shape prenatally present, or is it developed during the postnatal growth period? If so, what is the nature of the development of sexual dimorphism? Are the trajectories of vertebral size and shape variation during ontogeny different between males and females? Or is there only one trajectory observed but differences in size and shape are achieved through differences in growth period and growth rate between the sexes?

Another new approach to the investigation of hominoid lumbar vertebral size and shape is the analysis of the intra-specific variation of inter-segmental shape variation patterns along the lumbar spine. Differences in vertebral size and shape might be present between the sexes of a taxon. The investigation of patterns of inter-specific shape variation and immature specimens within each taxon is combined – where it is possible due to the availability of sufficient sample sizes (see material and method section of this chapter). If intra-specific differences in patterns of inter-segmental size and shape variation along the lumbar spine are established early on in ontogeny, this indicates that they are under genetic control. However, if these differences are established later in ontogeny, they are likely under less direct genetic controls and influenced by body weight and size or function (such as locomotion).

3.3.1 Aims of the present study and hypotheses

The aims of the study can be summarized as follows:

- The first goal is to confirm the presence or absence of any intra-specific differences in lumbar vertebral size and shape within each taxon in the study (*Homo sapiens, Gorilla gorilla, Pan troglodytes*, and *Pongo pygmaeus*).

If this is the case and intra-specific differences in vertebral size and shape are confirmed:

- The study will then investigate if differences in vertebral size and shape are related to sexual dimorphism in body weight. In case intra-specific differences in body weight cannot satisfactorily explain intra-specific differences in

vertebral size and shape, the potential relationship of intra-specific (sexual) differences in locomotor repertoires (weight transmission functions in relation to trunk position) and differences in vertebral size and shape will be investigated.

This study also examines:

- The extent to which patterns of inter-segmental shape variation along the lumbar spine differ between the sexes of the four hominoid taxa in the study and
- How sexual dimorphism in vertebral size and shape is established throughout postnatal ontogeny

Thus, the following hypotheses will be tested:

Hypothesis 1

The first hypothesis examines the extent to which there are intra-specific differences in lumbar vertebral size and shape within each taxon in the study.

- **Hypothesis 1.1:** There are no differences in vertebral centroid size between the sexes of the four hominoid taxa in the study

The hypothesis will be **falsified** if statistically significant differences in vertebral centroid size between the sexes are identified for one or more of the taxa in the study.

- **Hypothesis 1.2:** There are no differences in vertebral shape observed between the sexes of the four hominoid taxa in the study

This hypothesis will be **falsified** if statistically significant differences in vertebral shape between the sexes are identified for one or more taxa in the study.

Hypothesis 2

If there are intra-specific differences in vertebral size and shape observed within the taxa (hypothesis 1.1 and 1.2 falsified), the second hypothesis examines the extent to which the differences in size and shape relate to differences in body weight (sexual dimorphism) between the sexes.

- **Hypothesis 2.1:** There is no relationship between patterns of vertebral size variation and body weight variation between the sexes of each taxon in the study

- **Hypothesis 2.2:** There is no relationship between patterns of vertebral shape variation and body weight variation between the sexes of each taxon in the study

These sub-hypotheses will be tested by examining to what extent variation of vertebral size and shape within each taxon corresponds with differences in body weight between the sexes of each taxon.

Hypothesis 3

A further reason for differences in size and shape between the sexes within each taxon is differences in locomotor repertoires. The following hypotheses are constructed to allow a test of the impact of locomotion on sexual dimorphism.

- **Hypothesis 3.1:** There is no relationship between patterns of vertebral size variation and locomotor differences between the sexes of each taxon in the study

- **Hypothesis 3.2:** There is no relationship between patterns of vertebral shape variation and locomotor differences between the sexes of each taxon in the study

Hypothesis 4

Hypotheses 1 to 3 tested for the presence or absence of differences in patterns of size and shape variation within each taxon, based on single lumbar vertebrae. It is also of interest to consider how vertebral form varies along the lumbar vertebral column in each taxon, because this too potentially relates to differences in body weight. First, we aim to identify any intra-specific differences in inter-segmental shape variation between the taxa.

- Hypothesis 4: There are no differences in patterns of lumbar inter-segmental size and shape variation between the sexes within each taxon in the study

Hypothesis 5

If sexual differences in patterns of lumbar inter-segmental shape variation are present within one or more taxa, then the study aims to assess the extent to which these are related to either sexual differences in body weight or differences in locomotor repertoire (if observed).

- **Hypothesis 5.1:** There is no relationship between sexual dimorphism in patterns of inter-segmental size variation along the lumbar spine and vertebral size or body weight dimorphism

- **Hypothesis 5.2:** There is no relationship between sexual dimorphism in patterns of inter-segmental shape variation along the lumbar spine and sexual dimorphism in locomotor modes and repertoires

These sub-hypotheses will be falsified if there are relationships observed between the intra-specific differences in patterns of inter-segmental shape variation along the spine and intra-specific differences in body weight and locomotion respectively.

3.3.2 Further aim

An investigation of when and how intra-specific differences in vertebral size and shape and patterns of inter-segmental shape variation along the lumbar spine are established during postnatal ontogeny will be conducted.

The operationalization of the hypotheses above will be presented in the materials and methods section of this chapter.

3.4 Materials and Methods

3.4.1 Materials

Materials used in this study consist of lumbar vertebrae from immature and adult modern humans, the two African ape species, *Gorilla gorilla*, and *Pan troglodytes*, and the Asian great ape *Pongo pygmaeus*. For details of the provenance of these specimens, criteria for measurement and determination of stage of maturation, refer to the materials

section of Chapter II, materials and methods (from p. 94). Table 3.2 shows the total sample, split along taxon, sex, age, and number of lumbar vertebrae boundaries. However, table 3.2 also indicates that in some parts of this study, results might be influenced considerably by small or unbalanced sample sizes. For example, the human immature sample is very unbalanced (no female infants, no male sub-adults). Also, the total sample of *Pongo pygmaeus* is very small and results from exploring this sample are to be interpreted with caution.

Species	Sex	Adults	Sub-adults	Juveniles	Infants	Total
Gorilla gorilla	Males (L4 + L3)	**23** (17 +6)	**4**	**7**	**8**	**42**
	Females (L4 + L3)	**22** (14 + 8)	**3**	**10**	**8**	**43**
Pan troglodytes	Males (L4 + L3)	**18** (15 + 3)	**3**	**14**	**14**	**49**
	Females (L4 + L3)	**22** (13 + 9)	**2**	**8**	**11**	**43**
Pongo pygmaeus	Males (all L4)	**6**	**3**	**2**	**2**	**13**
	Females (all L4)	**6**	**1**	**1**	**1**	**9**
Homo sapiens	Males (all L5)	**26**	**-**	**2**	**2**	**30**
	Females (all L5)	**21**	**2**	**5**	**-**	**28**

Table 3.2 Hominoid sample sizes for each taxon divided by numbers of vertebrae, age, and sex. Numbers in parentheses (*Gorilla* and *Pan*) represent numbers of specimens with four and three lumbars respectively (L4 + L3)

3.4.2 Comparing adult African great ape specimens with different numbers of lumbar vertebrae

To be able to compare African ape specimens with different numbers of lumbar vertebrae the following approach was used. Specimens with only three lumbars usually have one sacral vertebra more. The number of thoracic vertebrae is in most case the same as in specimens with four lumbars: all usually have 13 thoracics. Therefore the first three lumbar elements are considered to be phylogenetic equivalents whereas L4 does not have an equivalent (see figure 3.1). This means that for the last lumbar

vertebra, the sample size is reduced by 30% in *Gorilla* and *Pan*. Since the total samples are large (45 adult *Gorilla* and 40 adult *Pan* specimens), the sample consisting only of specimens with four vertebrae was considered adequate for comparison. Figure 3.1 shows the respective lumbar vertebrae compared on each level.

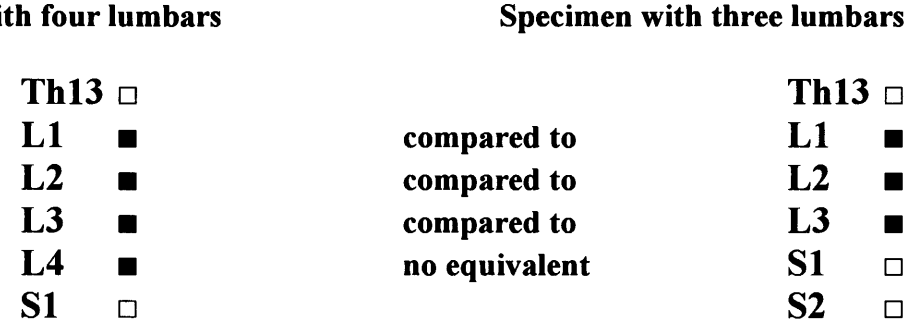


Figure 3.1 Comparison levels between African ape specimens with three and four lumbar vertebrae

3.4.3 Methods - general

Landmark definitions, landmark distribution, and landmark data collecting methods are described in detail in Chapter II, materials and methods (from p. 111). Statistical procedures (GPA/PCA; Procrustes distances, step-wise discriminant analysis, independent t-test, and permutation tests) employed in analysis 1 to 6 (see operationalizing hypotheses 1 to 6 below) are described in more detail in Chapter II, material and methods (from p. 125). In addition, for what purpose and in context with what analysis (1 to 6) they are employed is also described in operationalizing hypotheses 1.1 to 5.2.

3.4.4 Methods – operationalizing hypothesis 1.1 to 5.2

This study presents **five analyses** to test the five hypotheses formulated previously as follows:

Hypothesis 1.1: There are no differences in vertebral centroid size between the sexes of the four hominoid taxa in the study

In **analysis 1**, vertebral centroid sizes are compared between the sexes of each taxon at each comparison level (first to last lumbar). Independent t-tests are employed to investigate whether they are significantly different between the sexes. This hypothesis will be falsified if the results from analysis 1 yield statistically significant differences in vertebral size between the sexes of the taxa in the study.

Hypothesis 1.2: There are no differences in vertebral shape observed between the sexes of the four hominoid taxa in the study

To test for intra-specific differences in vertebral shape within each taxon, Procrustes mean distances are calculated between the shape configurations of female and male sub-samples of each taxon (**analysis 2**) at each comparison level. Permutation tests are used to calculate the significance of differences in shape between the sexes of each taxon. Hypothesis 1.2 is **falsified** if results from analysis 2 yield statistically significant differences in vertebral shape between the sexes of each taxon.

Hypothesis 2.1: There is no relationship between patterns of vertebral size variation and body weight variation between the sexes of each taxon in the study

To investigate relationships between the patterns of vertebral size variation and body weight between the sexes of each taxon in the study, results from **analysis 1** (centroid size), representing vertebral size will be compared with intra-specific differences in body weight (from the literature, see table 3.1) of each taxon. The hypothesis will be falsified if there is a relationship between intra-specific differences in body weight and vertebral size.

Hypothesis 2.2: There is no relationship between patterns of vertebral shape variation and body weight variation between the sexes of each taxon in the study

This hypothesis is tested by comparing the results from **analysis 2**, representing intra-specific differences in vertebral shape with intra-specific differences in body weight of each taxon. The hypothesis will be falsified if there is a relationship between differences in body weight and differences in vertebral shape between the sexes of each taxon in the study.

Hypothesis 3.1: There is no relationship between patterns of vertebral size variation and locomotor differences between the sexes of each taxon in the study

Hypothesis 3.1 tests for the presence or absence of relationships between intra-specific differences in vertebral size and locomotor repertoires of each taxon. Results from **analysis 1** (differences in centroid size), assessing differences in vertebral size between sexes of each taxon, are compared to intra-specific differences in locomotor repertoires, compiled from the literature. Hypothesis 3.1 cannot be statistically falsified because samples of individual body weights for the sample of vertebral size and shape data is not available. Instead of statistical falsification of hypothesis 3.1, an assessment of the *likelihood* that hypothesis 3.1 is false is attempted, based on the qualitative comparison of locomotor data with differences in vertebral size and shape between the sexes.

Hypothesis 3.2: There is no relationship between patterns of vertebral shape variation and locomotor differences between the sexes of each taxon in the study

Hypothesis 3.2 is tested for the presence of relationships between patterns of vertebral shape variation and intra-specific differences in locomotor repertoire within each taxon. To test hypothesis 3.2, intra-specific differences in vertebral shape are assessed in **analyses 3** (single specimens) and **4** (sexes mean shape). Methods consist of GPA/PCA and discriminant analysis and results are visualized with PC plots and thin spline grids. Results from analyses 3 and 4 and additionally 2 (permutation tests) are compared with intra-specific differences in locomotor repertoires. If there is a relationship between intra-specific differences in vertebral shape and locomotor repertoires, the hypothesis will be falsified.

Hypotheses 1.1 to 3.2 test intra-specific differences in lumbar vertebral size and shape between the taxa and external factors such as intra-specific differences in body weight and locomotor repertoires. Hypothesis 4, on the other hand, tests for differences in patterns of inter-segmental shape variation along the lumbar spine.

Hypothesis 4: There are no differences in patterns of lumbar inter-segmental size and shape variation between the sexes of each taxon in the study

Analysis 5 investigates intra-specific differences in patterns of inter-segmental size and shape variations (methods are the same as used for analysis 3 and 4 – GPA/PCA and plots of PCs). In the case of vertebral size differences, plots of mean vertebral centroid size (for each sex) vs. vertebral positions are produced. Hypothesis 4 is falsified if intra-specific differences exist within the patterns of inter-segmental shape variation along the lumbar spine of each taxon in the study. If hypothesis 4 is falsified (differences between the patterns of males and females of each taxon do exists), these differences will be further investigated by testing hypothesis 5.1 and 5.2.

- **Hypothesis 5.1:** There is no relationship between sexual dimorphism in patterns of inter-segmental size variation along the lumbar spine and vertebral size or body weight dimorphism

Hypothesis 5.1 tests for the presence or absence of a relationship between the patterns of inter-segmental size and shape variation along the lumbar spine and body weight variation between the sexes of each taxon. Hypothesis 5.1 will be tested by comparing the results from analysis 5 (differences in patterns) with those from analysis 1 (differences in vertebral centroid size) and with intra-specific differences in body weight from the literature. The hypothesis will be falsified if a relationship exists between patterns of inter-segmental size or shape variation and the intra-specific differences in body weight within each taxon in the study.

- **Hypothesis 5.2:** There is no relationship between sexual dimorphism in patterns of inter-segmental shape variation along the lumbar spine and sexual dimorphism in locomotor modes and repertoires

Hypothesis 5.2, tests for the presence or absence of a relationship between differences in inter-segmental shape variation along the lumbar spine between the sexes of each taxon and intra-specific differences in locomotion (kinematics of modes or proportions of different modes in repertoires). The hypothesis will be tested by comparing results from analysis 5 with the differences observed within the locomotor repertoires of each taxon (compiled from the literature). The hypothesis will be falsified if there is no relationship between the differences in patterns of intersegmental shape variation and locomotor repertoires within each taxon.

3.4.5 Assessment of ontogenetic development of intra-specific differences in patterns of inter-segmental shape variation along the lumbar spine

Finally, if hypothesis 4 is falsified, the development of intra-specific differences in patterns of inter-segmental shape variation along the lumbar spine will be further investigated. Samples of younger (infants) and older (juvenile) sub-adult specimens will be explored to see when and how these differences are established during postnatal ontogeny. To assess intra-specific differences in trajectories GPA/PCA analysis is performed on samples of each taxon, consisting of immature (infant, juvenile, subadult) and mature (adult) specimens.

3.5. Results

3.5.1 Analysis 1: assessing sexual dimorphism in lumbar vertebral size

Differences in vertebral size between the sexes of each taxon are explored by calculating the difference between the mean male and female vertebral centroid size at each comparison level. The mean male and female vertebral centroid sizes (and 2sd, as a proxy for the 95% confidence intervals) are presented in table 3.3. Independent T-tests were used to assess the significance of differences in vertebral centroid sizes between the sexes at each comparison level. The results from this analysis are presented in table 3.4.

These results indicate that – with the exception of the last lumbar vertebra of *Pan* - all vertebrae of all taxa in the study are highly significantly different in size between the sexes. Of all taxa in the study, *Gorilla* and *Pongo* show the highest degree of sexual dimorphism in vertebral centroid size at all comparison levels (see table 3.4). In *Pan,* significant differences in vertebral centroid size between the sexes are the smallest recorded. At comparison levels 1 to 3 (L1 to L3), sexual dimorphism in centroid size is highly significant ($p>0.01$). However, the last *Pan* lumbar vertebra is not significantly different in mean centroid size between the sexes. Finally, the lumbar vertebrae of *Homo sapiens* are highly significantly different in vertebral centroid size between males and females at all comparison levels.

Taxon	L1	L2	L3	L4	L5
Gorilla gorilla ♂	**9.3688** ± 1.1328 (1sd = 0.5664)	**9.2323** ± 1.5442 (1sd = 0.7721)	**9.2997** ± 0.9836 (1sd = 0.4918)	**8.8452** ± 1.0204 (1sd = 0.5102)	
Gorilla gorilla ♀	**7.6454** ± 0.8672 (1sd = 0.4336)	**7.6523** ± 0.8134 (1sd = 0.4067)	**7.5803** ± 0.9276 (1sd = 0.4638)	**7.2023** ± 0.6836 (1sd = 0.3418)	
Pan troglodytes ♂	**6.8021** ± 0.6266 (1sd = 0.3133)	**7.1760** ± 0.6820 (1sd = 0.341)	**7.0925** ± 0.6026 (1sd = 0.3013)	**6.7620** ± 0.4886 (1sd = 0.2443)	
Pan troglodytes ♀	**6.5234** ± 0.6252 (1sd = 0.3126)	**6.7448** ± 0.5614 (1sd = 0.2807)	**6.7427** ± 0.270 (1sd = 0.1350)	**6.5495** ± 0.8864 (1sd = 0.4432)	
Pongo pygmaeus ♂	**7.4098** ± 0.5798 (1sd = 0.2899)	**7.5786** ± 0.5468 (1sd = 0.2734)	**7.4614** ± 1.4266 (1sd = 0.7133)	**7.4670** ± 0.7958 (1sd = 0.3979)	
Pongo pygmaeus ♀	**6.2578** ± 0.3758 (1sd = 0.1876)	**6.3010** ± 0.6238 (1sd = 0.3119)	**6.3510** ± 0.688 (1sd = 0.3440)	**6.2278** ± 0.284 (1sd = 0.1420)	
Homo sapiens ♂	**7.9714** ± 0.8966 (1sd = 0.4483)	**8.3378** ± 0.8614 (1sd = 0.4307)	**8.6042** ± 0.959 (1sd = 0.4795)	**8.7382** ± 0.546 (1sd = 0.2730)	**9.0939** ± 1.0134 (1sd = 0.5067)
Homo sapiens ♀	**7.3488** ± 0.8272 (1sd = 0.4136)	**7.6983** ± 0.7726 (1sd = 0.3863)	**7.9049** ± 0.7662 (1sd = 0.3831)	**7.9633** ± 0.786 (1sd = 0.3930)	**8.3327** ± 0.8578 (1sd = 0.4289)

Table 3.3 Tabulation of vertebral centroid sizes. Modern taxa: mean sizes ± 2 sds (serves as proxy for 95%interval). Second line = 1 sd

The intra-specific differences in human centroid size are not as big as those observed between male and female *Gorilla* and *Pongo* but they are bigger than those observed in *Pan*. In contrast to the great apes, where the differences in centroid size between the sexes at each comparison level remain fairly constant, in humans they increase gradually towards the sacrum. Thus L4 and L5 differ more in centroid size between the sexes than do L1, L2, and L3.

Species	L1	L2	L3	L4	L5
Homo sapiens	**0.6226**	**0.6337**	**0.6993**	**0.7786**	**0.7612**
Males vs. females	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**
Gorilla gorilla	**1.7233**	**1.5882**	**1.7194**	**1.6429**	
Males vs. females	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	
Pan troglodytes	**0.3380**	**0.4312**	**0.3574**	0.2125	
Males vs. Females	**p=0.003**	**p=0.001**	**p=0.002**	p=0.115	
Pongo pygmaeus	**1.115**	**1.3833**	**1.267**	**1.239**	
Males vs. females	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	

Table 3.4 Sexual dimorphism in vertebral centroid size. Line 1: difference in mean centroid size between sexes (in cm), line 2: level of significance, tested with independent t-test. Highlighted values are significant at the level $p<0.001$. These are even significant taking into account Bonferroni corrections (significance tests n = 17, familywise error = 58.1%, p-Bonferroni corrected = 0.003)

There are no body weight data available for any of the specimens in the present study. Therefore, significance tests cannot be conducted on the relationship between sexual dimorphism in body weight and centroid size intra-specifically. Nevertheless, a comparison of differences in body weight (shown as ♂/♀ ratio) between the sexes with sexual dimorphism in vertebral size (centroid size) at each vertebral level is shown in table 3.5.

The comparison in table 3.5 shows that *Pongo* has the largest ♂/♀ weight ratio and the second largest vertebral centroid size dimorphism. In *Gorilla*, the second largest ♂/♀ weight ratio is paired with the largest sexual dimorphism in vertebral centroid size differences and ratios. *Pan*, on the other hand, has the second smallest ♂/♀ weight ratio and shows the smallest differences in vertebral centroid size differences and ratios between the sexes. Thus, in great apes, there is a strong relationship between sexual dimorphism in body weight and vertebral size. *Homo sapiens*, interestingly is the odd

one out: here the smallest ♂/♀ weight ratio is combined with a sexual dimorphism in centroid size which by far exceeds that seen in *Pan.*

Sexual dimorphism	*Homo sapiens*	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*
♂/♀ weight ratio	1.2	1.95	1.3	2.0
Centroid size L1	0.6226	1.7233	0.3380	1.115
Centroid size L2	0.6337	1.5882	0.4312	1.3833
Centroid size L3	0.6993	1.7294	0.3574	1.267
Centroid size L4	0.7786	1.6429	0.2125	1.239
Centroid size L5	0.7612			

Table 3.5 Comparison of sexual dimorphism in mean body weight (presented as ♂/♀ weight ratio), differences in mean centroid size (cm), and ♂/♀ centroid size ratio at each vertebral level

3.5.2 Analysis 2: assessing sexual dimorphism in lumbar vertebral shape

To investigate the potential presence of sexual dimorphism in the lumbar vertebral shape of the hominoid taxa in the study, Procrustes distances were calculated between the sexes of each taxon and at each comparison level. Permutation tests were used to assess the significance of the Procrustes distances between the sexes. These results are displayed in table 3.6.

The results indicate that *Homo sapiens* and *Gorilla* show highly significant levels of sexual dimorphism in vertebral shape at all vertebral comparison levels - with the exception of the last lumbar vertebra in *Gorilla*. *Homo sapiens* exceeds *Gorilla* in the degree of shape differences and actually shows the highest degree of all taxa in the study (excluding the results for *Pongo* but see next paragraph). None of the *Pan* lumbar vertebrae are significantly different in shape between the sexes (see table 3.6). Despite the rather large degree of sexual dimorphism observed in vertebral centroid size (table 3.4), differences in shape are not significant between male and female *Pongo* specimens. Nevertheless, values for Procrustes distances are very high when compared with the other taxa in the same table (see table 3.5). An explanation for the low levels of

significance observed in table 3.5 might be related to the small sample sizes of *Pongo* (n = 5 and 6 respectively for males and females). The considerable amount of shape variation (large Procrustes distance) between the sexes too might be over estimated due to the small sample sizes.

Species	L1	L2	L3	L4	L5
Homo sapiens	**0.068**	**0.0656**	**0.0702**	**0.0697**	**0.0696**
n = 47 (L5)	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**
Gorilla gorilla	**0.0609**	**0.0503**	**0.0597**	0.0573	
n = 55 (L1-L3)	**p =0.001**	**p=0.009***	**p=0.001**	p=0.1046	
n = 36 (L4)					
Pan troglodytes	0.0455	0.0379	0.0364	0.046	
n = 40 (L1-L3)	p=0.1949	p=0.3219	p=0.7628	p=0.625	
n = 30 (L4)					
Pongo pygmaeus	0.075	0.0878	0.0878	0.0902	
n=12 (L4)	p=0.234	p=0.284	p=0.297	p=0.3199	

Table 3.6 Sexual dimorphism in vertebral shape, represented by Procrustes distances. Line 1: Procrustes distances, line 2: level of significance, tested with Permutation tests (1000 iterations). Highlighted values are significant at level $p<0.001$. All tests remain significant with Bonferroni corrections except * (significance tests n = 17, familywise error = 58.1%, p-Bonferroni corrected = 0.003)

To assess the relationship between vertebral shape and body weight, a comparison of sexual dimorphism in body weight and vertebral shape (represented by Procrustes distances between mean male and female vertebral shape, see table 3.6) is shown in table 3.7. The comparison in table 3.7 shows that *Pongo* has the largest sexual dimorphism (might be distorted due to small sample size) in vertebral shape and the largest ♂/♀ weight ratio. Humans and *Gorilla* show similar degrees of sexual dimorphism in vertebral shape but their ♂/♀ weight ratio. In *Pan*, on the other hand, the second smallest ♂/♀ weight ratio is combined with the smallest sexual shape dimorphism. These findings indicate that in general, the relationship between sexual dimorphism in body weight and vertebral shape is weaker than that observed between sexual dimorphism in body weight and vertebral size (table 3.5).

Sexual dimorphism	*Homo sapiens*	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*
♂/♀ weight ratio	1.2	1.95	1.3	2.0
Procrustes distances L1	0.068	0.0609	0.0455	0.075
Procrustes distances L2	0.0656	0.0503	0.0379	0.0878
Procrustes distances L3	0.0702	0.0597	0.0364	0.0878
Procrustes distances L4	0.0697	0.0573	0.046	0.0902
Procrustes distances L5	0.0696			

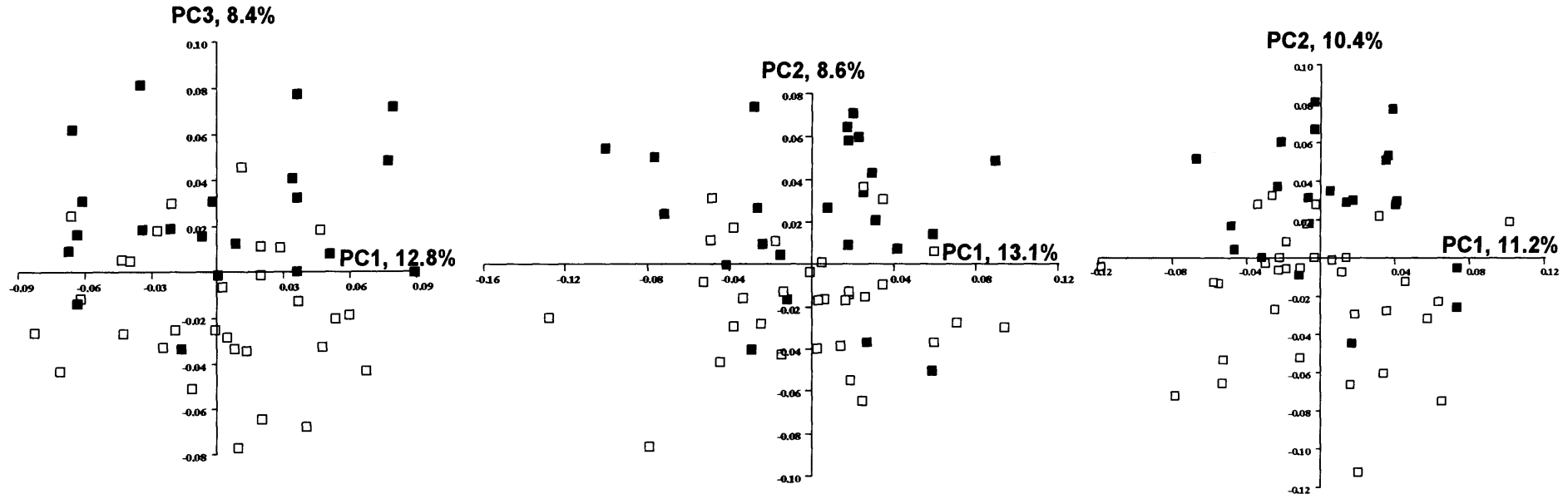
Table 3.7 Comparison of sexual dimorphism in mean body weight (presented as ♂/♀ weight ratio) and mean vertebral shape (Procrustes distances, in cm) at each vertebral level

3.5.3 Analysis 3: sexual dimorphism in vertebral shape – full adult sample analysis

To further explore the intra-specific differences in vertebral shape discovered by comparing the Procrustes mean distances between the sexes of each taxon, the landmark data were explored with GPA/PCA. Analysis 3 investigates sexual dimorphism in vertebral shape within the total adult samples of each taxon. Step-wise discriminant analysis was used to identify the strongest sex discriminators and scatter plots of these PCs vs. PC1 (strongest discriminators for total shape variation within a taxon) are displayed. It has to be kept in mind that not only the first few PCs (e.g. PC1 to 5) summarize significant aspects of sexual shape dimorphism. These are also spread out across higher PCs. Nevertheless, visualization is sometimes difficult, because sexual dimorphism is at an angle to the plotted PCs in the figures (i.e. these differences are not lined up with e.g. PC2 or 3 etc). Each taxon is presented separately.

Gorilla gorilla

The results from analysis 2 (permutation tests, table 3.6) indicate that *Gorilla* specimens with four lumbar vertebrae are sexually dimorphic in shape except for the last lumbar vertebra. Specimens with only three free lumbar vertebrae were sexually dimorphic for all three vertebrae. Thus, only vertebrae L1 to L3 are considered for further analysis of sexual dimorphism in lumbar vertebral shape.



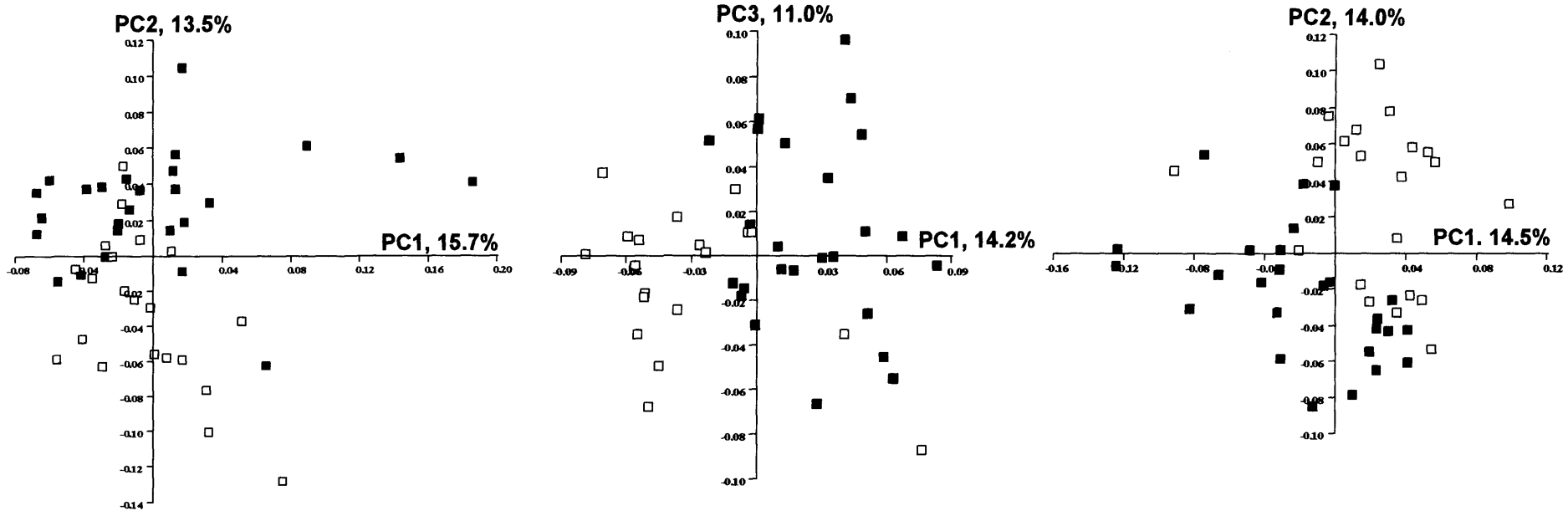
A: First lumbar vertebra **B:** Second lumbar vertebra **C:** Third lumbar vertebra

Figure 3.2 Scatter plots of PC1 vs. strongest sex discriminators. Adult *Gorilla gorilla* sample **(A)** comparison level 1 (L1) **(B)** comparison level 2 (L2) **(C)** comparison level 3 (L3) ■ = males; □ = females

Figure 3.2 shows plots of PC1 versus the strongest sex discriminators at comparison levels 1 to 3. In the case of L1, PC3 is the strongest discriminator between the sexes, whereas for L2 and L3, PC2 is the strongest sex discriminator. Although results from analysis 2 are highly significant for vertebrae L1 to L3, the separation between the sexes along the axes of PCs 1 and the strongest sex discriminators is not very strong. Morphing the shape configurations along the axis of PC1 (12.8% tsv) at comparison level 1 (L1) shows that shape differences summarised by PC1 mainly represent differences between thoracic type and lumbar type first lumbar vertebrae. At comparison levels 2 and 3, the differences in shape summarized by PC1 (12.7% and 11.2% TSV respectively) could not be attributed to either differences in shape between sexes or other causes such as at comparison level 1.

Homo sapiens

According to the results of analysis 1 (sexual dimorphism in vertebral centroid size) and analysis 2 (sexual dimorphism in vertebral shape), lumbar vertebrae of *Homo sapiens* are highly sexually dimorphic in size and shape. Exploring landmark data of the total adult human sample with GPA/PCA and step-wise discriminant analysis results in scatter plots of PC1 versus the strongest sex discriminators (see figures 3.3 and 3.4). Step-wise discriminant analyses identified PC2 at comparison levels 1, 3, and 5, and PC3 at comparison levels 2 and 4 as the strongest sex discriminators. Percentages of total shape variation summarized by PC1 and PC2 and PC1 and PC3 respectively are displayed in figures 3.3 and 3.4. The overlap of female and male specimens is less than that observed previously in *Gorilla* but it is still quite substantial. As seen in *Gorilla*, at comparison level 1, PC1 summarizes differences in shape between thoracic-shaped first lumbars and lumbar-shaped first lumbar vertebrae. At comparison level 5 (last lumbar) differences in shape summarized by PC1 are attributed to differences in the degree of sacralization of the last lumbar vertebra.

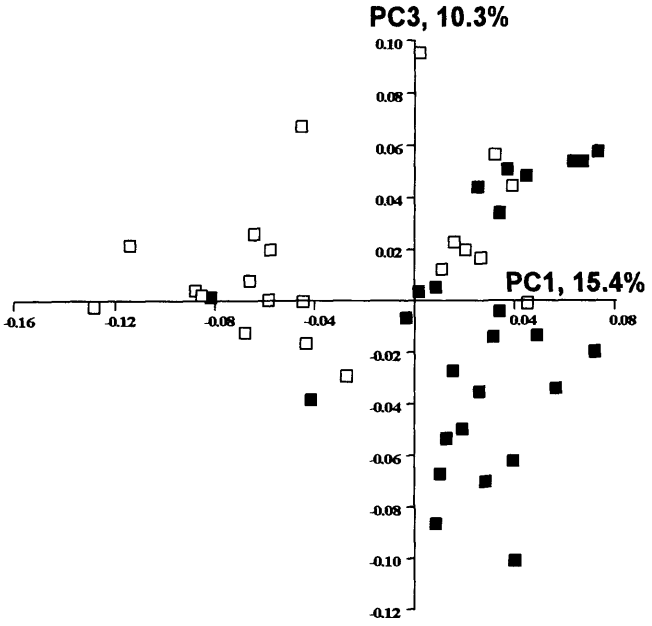


A: First lumbar vertebra

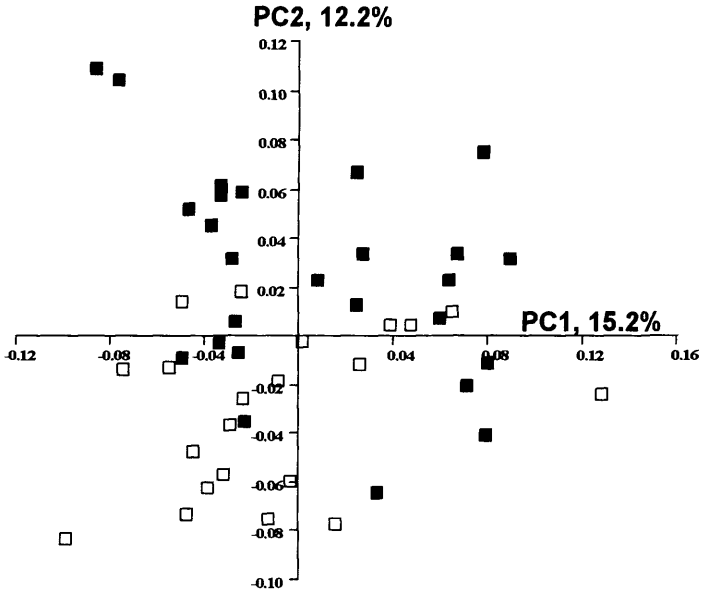
B: Second lumbar vertebra

C: Third lumbar vertebra

Figure 3.3 Scatter plots of PC1 vs. strongest sex discriminators. Adult *Homo sapiens* sample **(A)** comparison level 1 (L1) **(B)** comparison level 2 (L2) **(C)** comparison level 3 (L3) ■ = males; □ = females



A: Fourth lumbar vertebra



B: Fifth lumbar vertebra

Figure 3.4 Scatter plots of PC1 vs. strongest sex discriminators. Adult *Homo sapiens* sample **(A)** comparison level 4 (L4) **(B)** comparison level 5 (L5) ■ = males; □ = females.

Pan troglodytes

Table 3.6, summarizing the results from analysis 2 (sexual dimorphism in vertebral shape) shows that none of the lumbar vertebrae of *Pan* is significantly sexually dimorphic in shape. Nevertheless, GPA/PCA and step-wise discriminant analyses were conducted on the full adult sample of *Pan* of landmark data to confirm this. The analyses failed to separate male and female samples entirely. Therefore, no more analyses to explore differences in vertebral shape between the sexes were conducted on *Pan*.

Pongo pygmaeus

According to the results from analysis 2 (sexual dimorphism in vertebral shape, table 3.6), differences in vertebral shape between the sexes of *Pongo pygmaeus* are non-significant. However, the sexual dimorphism observed in vertebral size is substantial (see table 3.3 analysis 1and 3.4). Therefore, the adult *Pongo* sample was nonetheless analysed with GPA/PCA at each comparison level and step-wise discriminant analyses were performed to identify potential sex discriminators among the PCs yielded by the GPA/PCA analyses. The results show that - except for the last lumbar vertebra, L4 - step-wise discriminant analyses were able to identify PCs at each comparison level (L1 to L3) which are very successful at separating the sexes based on vertebral shape differences. There is a discrepancy between the results from the Procrustes distance analysis and the results from the GPA/PCA/step-wise discriminant analyses. This is probably due to the small *Pongo* sample size.

3.5.4 Analysis 4, shape differences between the sexes: mean shapes at each comparison level

Analysis 3 explored large samples of adult lumbar vertebral landmark configurations at each comparison level. The resulting shape space is high dimensional and differences between mean shapes are to some extent obscured by differences between individuals within each taxon (intra-specific variation). In the case of *Pongo*, results from analysis 3 are difficult to interpret because of the very small sample size.

In order to reduce dimensionality and to be able to directly compare differences in shape between sex means for *Gorilla*, *Homo sapiens*, and *Pongo*, further GPA/PCA analyses were carried out on sex mean data at each comparison level. Thus, the mean male and female shapes of each vertebra were calculated and then analyzed with GPA/PCA. The analysis of only two shapes (sex means) yields only one PC. PC1 therefore represents the total shape variance between mean males and females. These differences in shape between the sexes are visualized by warping the overall means to the extremes along the axis of PC1 thus producing superimposed transformation grids in three planes (thin spline planes). Mean female shapes were chosen to serve as the reference shapes, mean male shapes as target shapes. In addition, the overall mean lumbar vertebral shape has been calculated from all lumbar vertebrae (e.g. L1 to L5 in humans) for both sexes of each taxon in the study. These shapes are presented for each taxon and annotated with numbers to make it easier to follow the summaries of sexual shape dimorphism in each taxon. Results of analysis 4 are presented separately for each taxon.

Gorilla gorilla

The most obvious differences in shape between male and female *Gorilla* are observed in the dimensions of the vertebral bodies. *Gorilla* males have relatively shorter, in the medio-lateral direction (hereafter referred to as m-l) broader, vertebral bodies (①, figure 3.8). They are also relatively shorter in dorso-ventral dimensions. Male lumbar vertebral bodies show relatively more anterior wedging than female ones (figures 3.5 to 3.7 and 3.8). This anterior wedge shape of the male vertebral bodies is accompanied by a smaller inferior to superior body endplate, giving the male vertebral bodies a funnel shaped appearance. The dimensions and orientations of the grid distortions visible in figure 3.8 also indicate that males have a relatively taller, longer, and more downward (caudally) orientated spinous process (⑤, figure 3.8) and relatively shorter, broader male pedicles (②, figure 3.8). In relation to pedicle dimensions, the male vertebral foramen has a relatively smaller diameter than that of females (③, figure 3.8). Costal processes are moderately relatively longer in males than females (④, figure 3.8). This is mostly expressed at comparison level 3 (see figure 3.7). The *Incisura vertebralis major* of male gorillas is relatively narrower than the female ones (⑧, figure 3.8). Finally, both, superior and inferior articular facets are moderately more horizontally orientated in females than males (⑦, figure 3.8).

At comparison level 1 (L1), these intra-specific differences in shape create the impression that males have more lumbar type first lumbar vertebrae whereas the female first lumbar vertebrae still resemble thoracic vertebrae relatively strongly. The superior articular processes of the female first lumbars are more horizontally orientated, the vertebral arches are relatively broader and the costal processes are relatively shorter – which makes them resemble thoracic vertebrae more. At comparison level 3, the male spinous process is most different between the sexes (figure 3.7) and the *Incisura vertebralis major* is the relatively narrowest at all comparison levels.

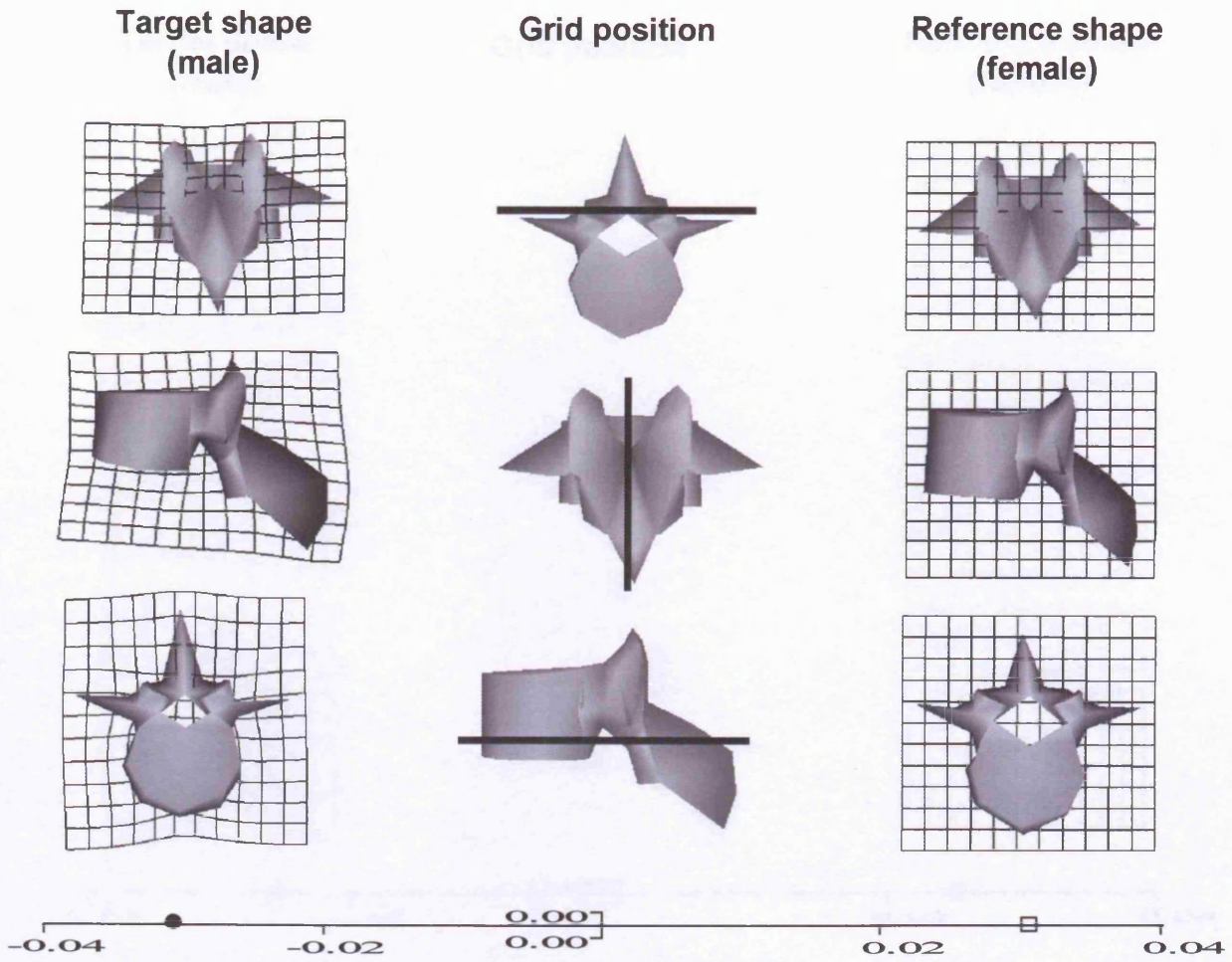


Figure 3.5 Sexual dimorphism in mean lumbar vertebral shape (L1), *Gorilla gorilla*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

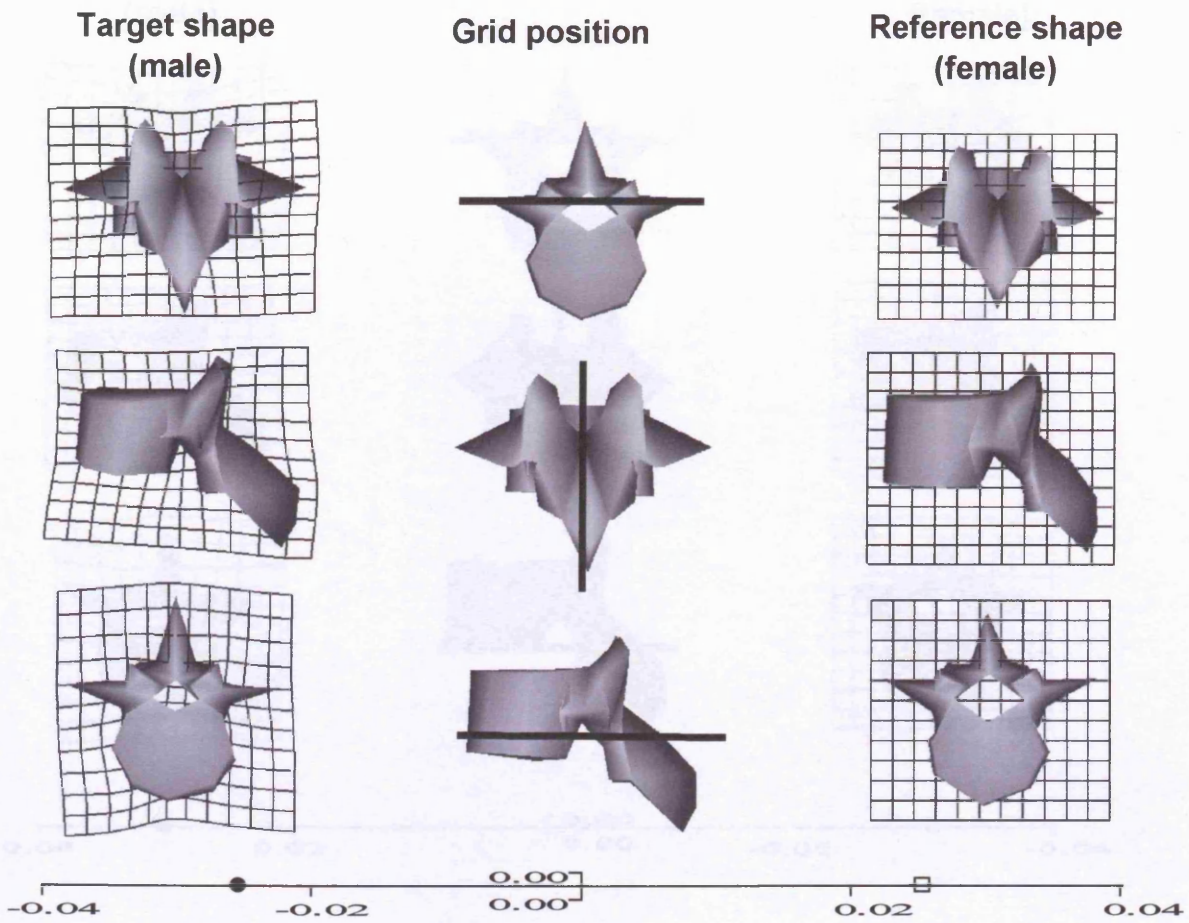


Figure 3.6 Sexual dimorphism in mean lumbar vertebral shape (L2), *Gorilla gorilla*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

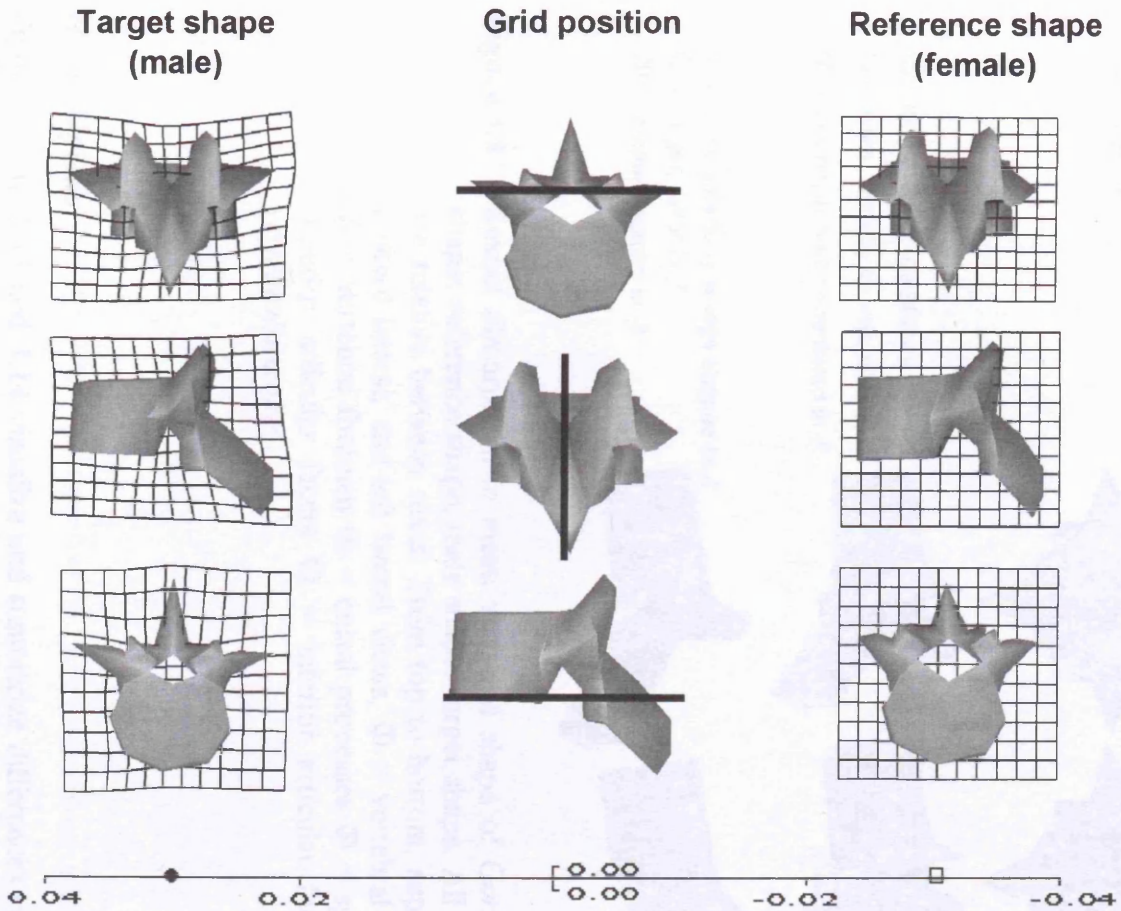


Figure 3.7 Sexual dimorphism in mean lumbar vertebral shape (L3), *Gorilla gorilla*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

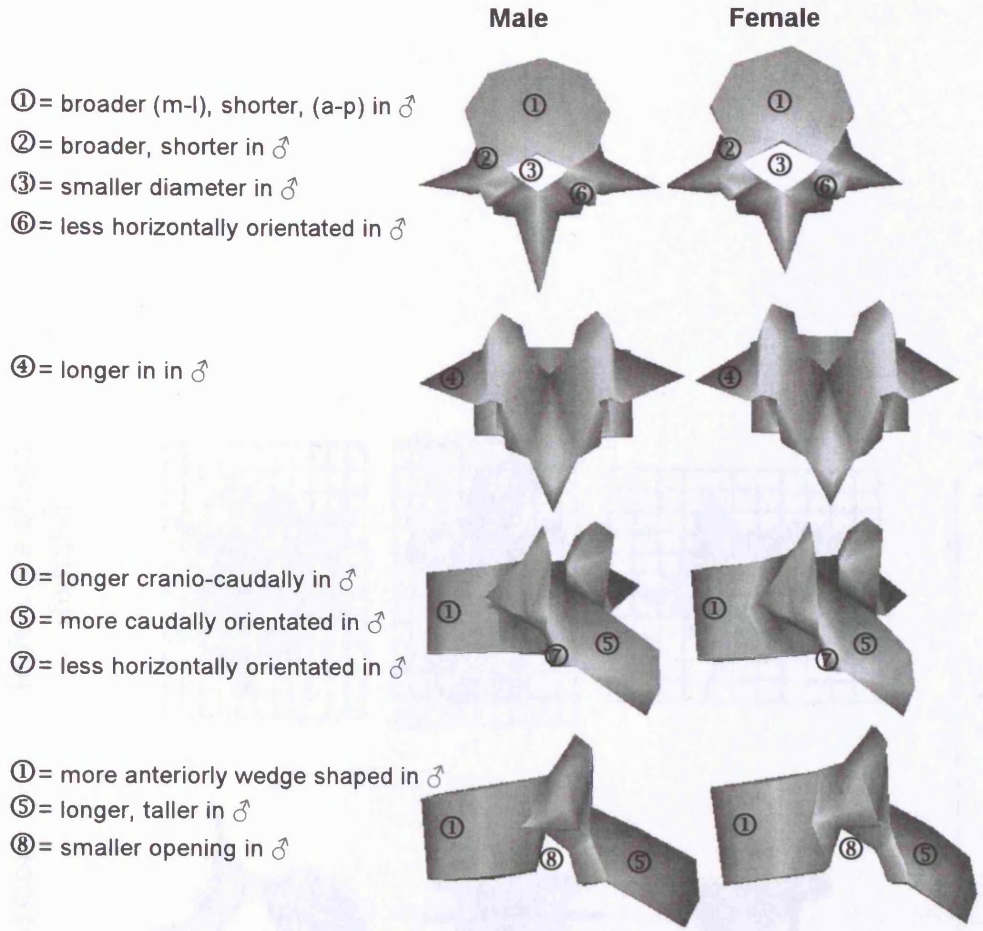


Figure 3.8 Sexual dimorphism in mean vertebral shape of *Gorilla gorilla*. Female shape: reference shape, male shape: target shape. All differences in shape are relative between sexes. From top to bottom: superior, posterior, left postero-lateral, and left lateral views. ① = vertebral body ② = pedicles ③ = vertebral foramen ④ = costal processes ⑤ = spinous process ⑥ = superior articular facets ⑦ = inferior articular facets ⑧ = *Incisura vertebralis major*

Homo sapiens

Figures 3.9 to 3.13 and 3.14 visualize and summarize differences in shape between the sexes of *Homo sapiens*. Humans are similar to *Gorilla* in that most differences in shape between the sexes are observed in the dimensions of the vertebral bodies. Males have relatively shorter, medio-laterally relatively broader and antero-posteriorly relatively shorter vertebral bodies. Female vertebral bodies, on the other hand, are more posteriorly wedge shaped than male ones (see figures 3.11 to 3.13 and ①, 3.14). These differences in vertebral body shape become more accentuated at comparison levels 4 and 5 (penultimate and ultimate lumbar vertebrae).

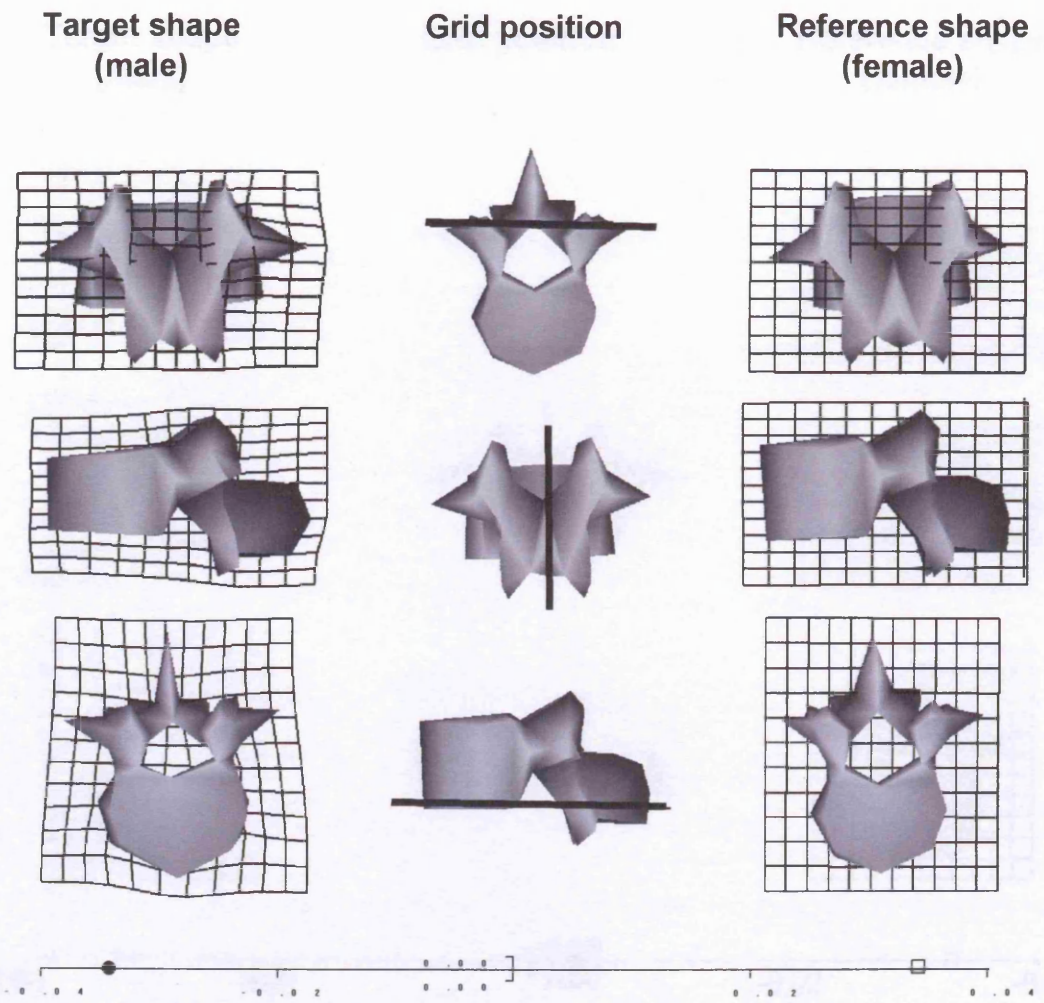


Figure 3.9 Sexual dimorphism in mean lumbar vertebral shape (L1), *Homo sapiens*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

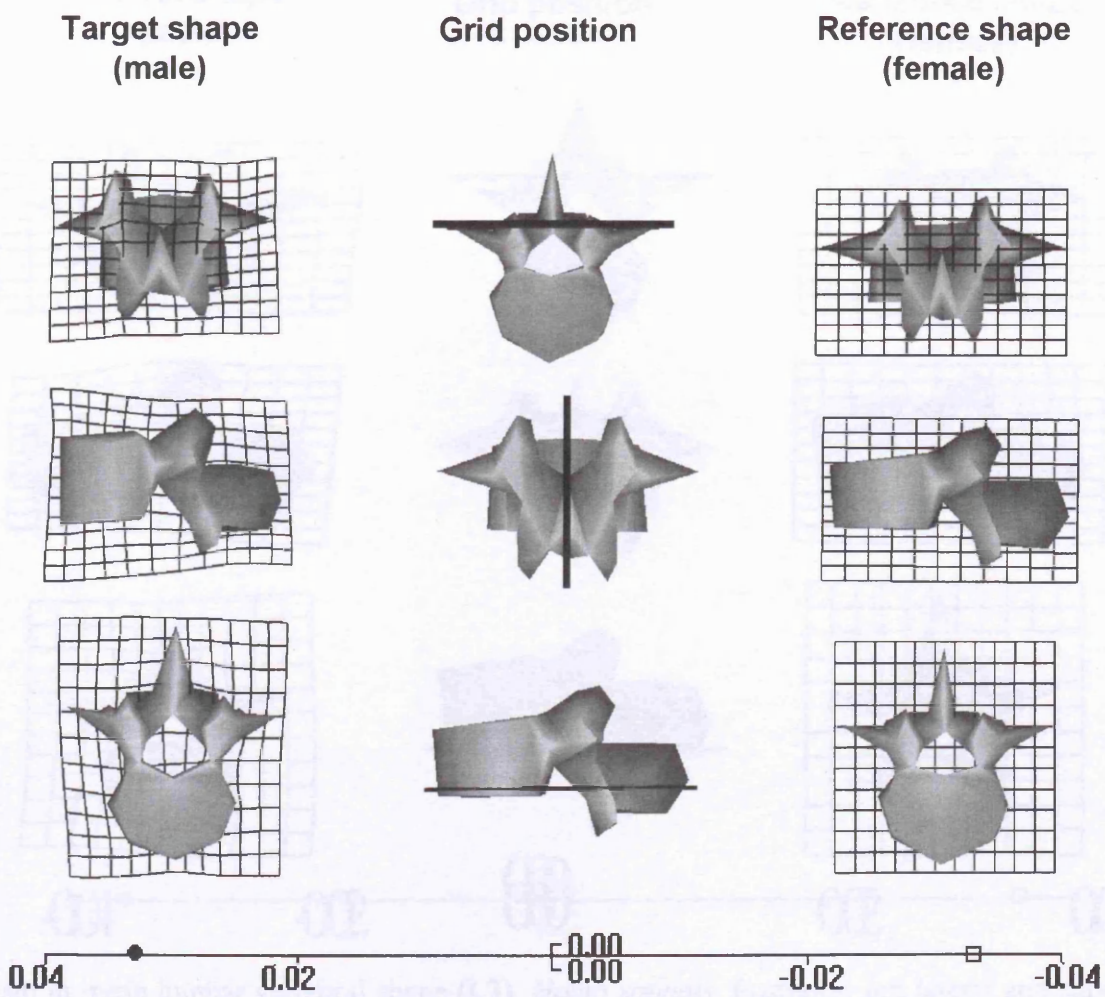


Figure 3.10 Sexual dimorphism in mean lumbar vertebral shape (L2), *Homo sapiens*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

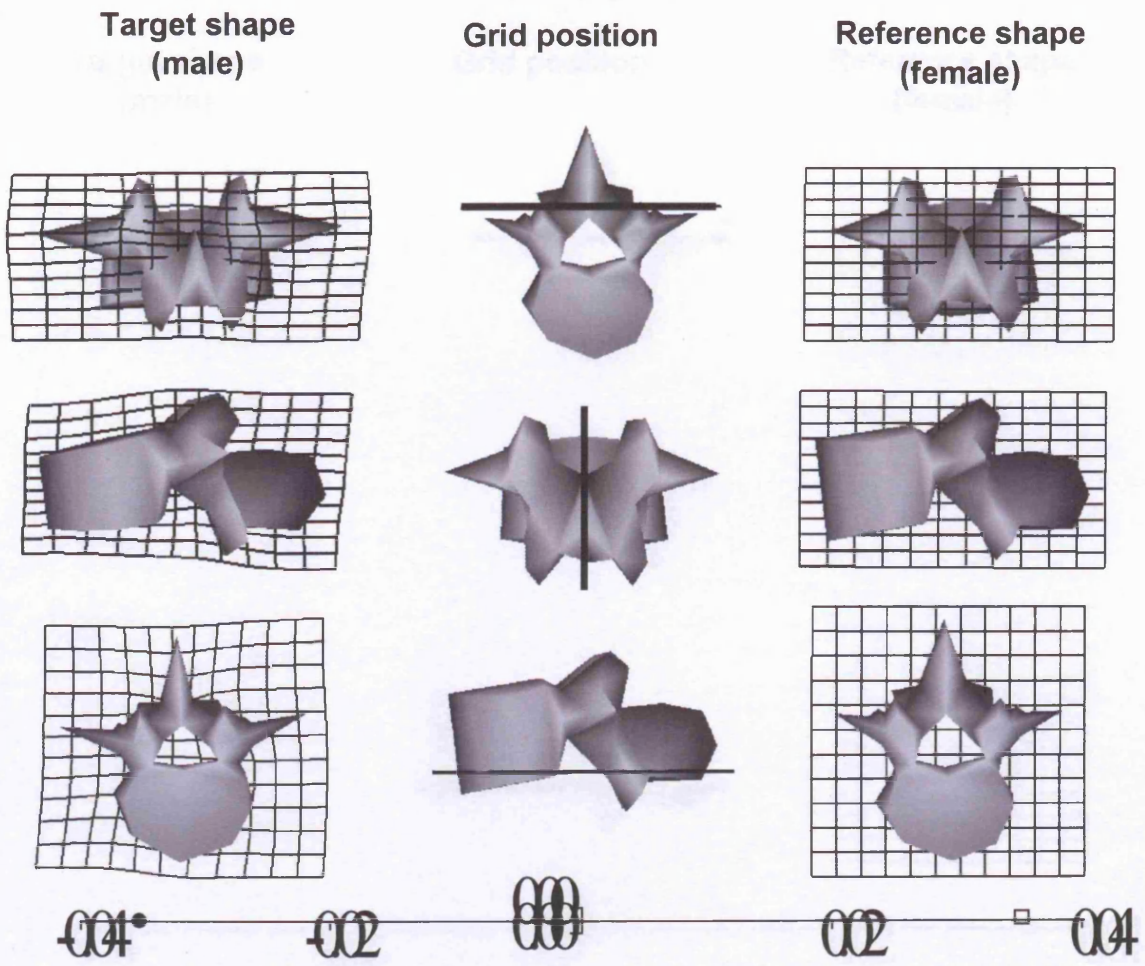


Figure 3.11 Sexual dimorphism in mean lumbar vertebral shape (L3), *Homo sapiens*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

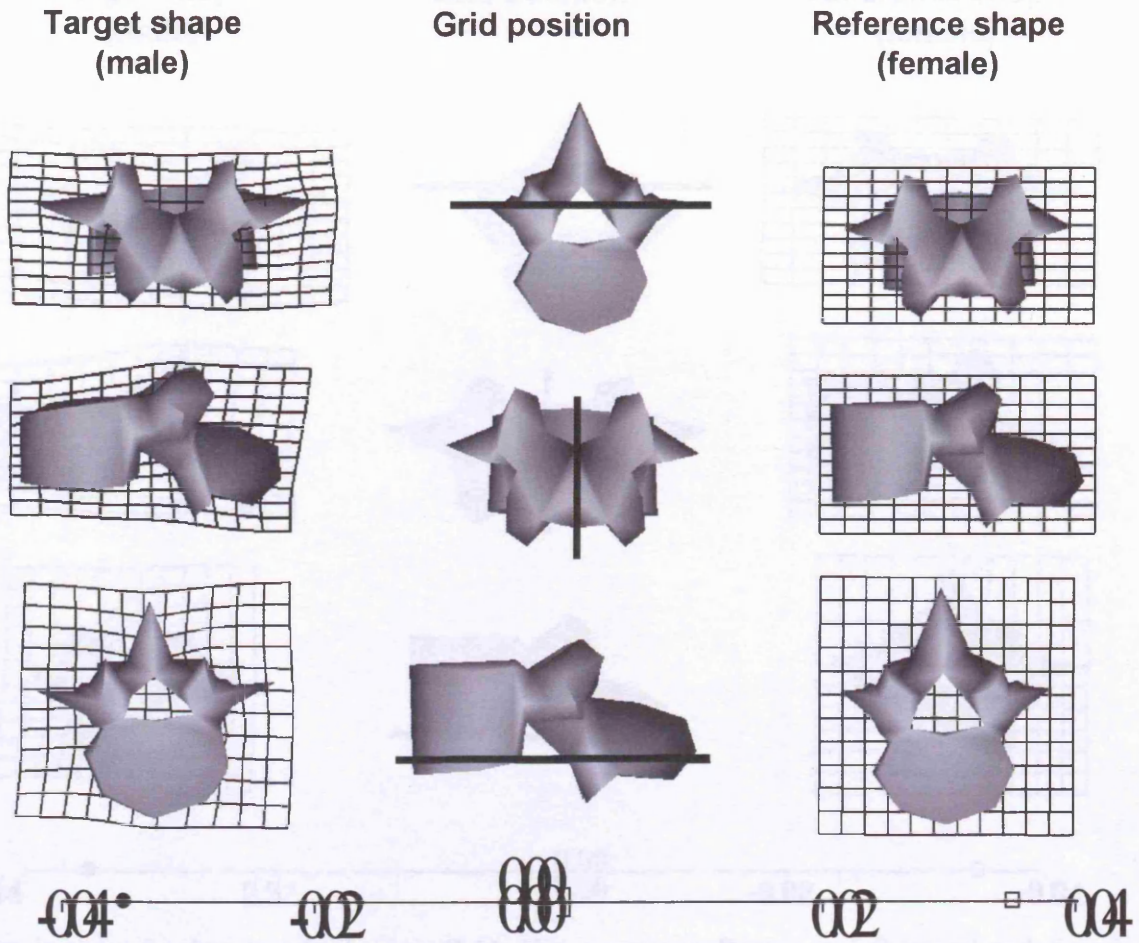


Figure 3.12 Sexual dimorphism in mean lumbar vertebral shape (L4), *Homo sapiens*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

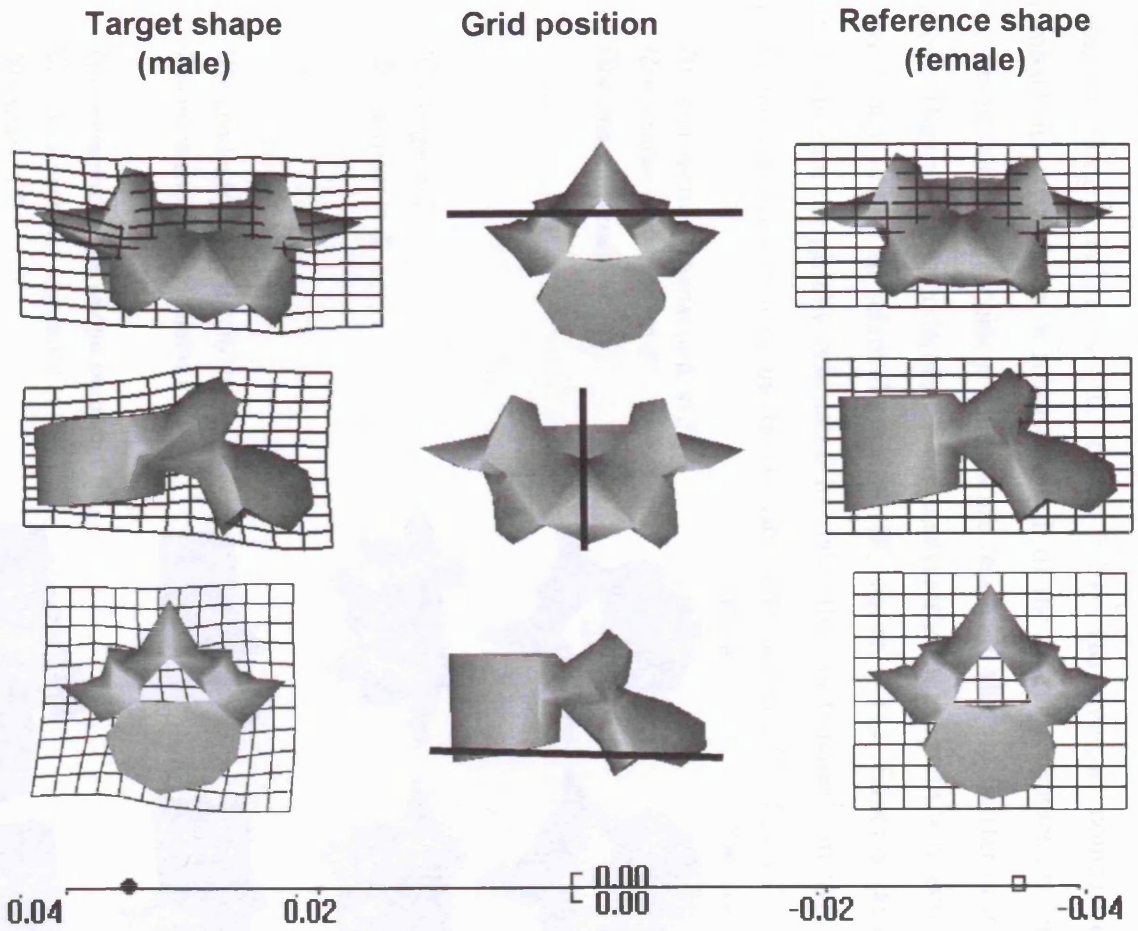


Figure 3.13 Sexual dimorphism in mean lumbar vertebral shape (L5), *Homo sapiens*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

At these same two levels plus comparison level 3, female vertebral bodies are clearly posteriorly wedge shaped whereas males are not (see figures 3.12 and 3.13). The male pedicles are relatively shorter and broader than the female ones (①, figure 3.14). At comparison level 5 (last lumbar), differences in relative pedicle length between the sexes are very small, but differences in relative pedicle width persist on this comparison level. In relation to differences in pedicle dimension between the sexes, males have relatively narrower and shorter vertebral foramina (②, figure 3.14). The vertebral arch is relatively narrower in males than in females (⑤, figure 3.14). The costal processes are relatively longer in males (④, figure 3.14). However at comparison level 5 (last lumbar), no differences in relative length of the costal processes are observed between the sexes. Inferior articular processes are relatively slightly shorter in females (⑦, figure 3.14). They are also moderately more posteriorly angled and the opening of the *Incisura vertebralis major* is relatively wider (⑧, figure 3.14). Superior articular facets are relatively more sagittally orientated in males than in females. Finally, the male spinous process is relatively shorter and taller than the female one (⑨, figure 3.14).

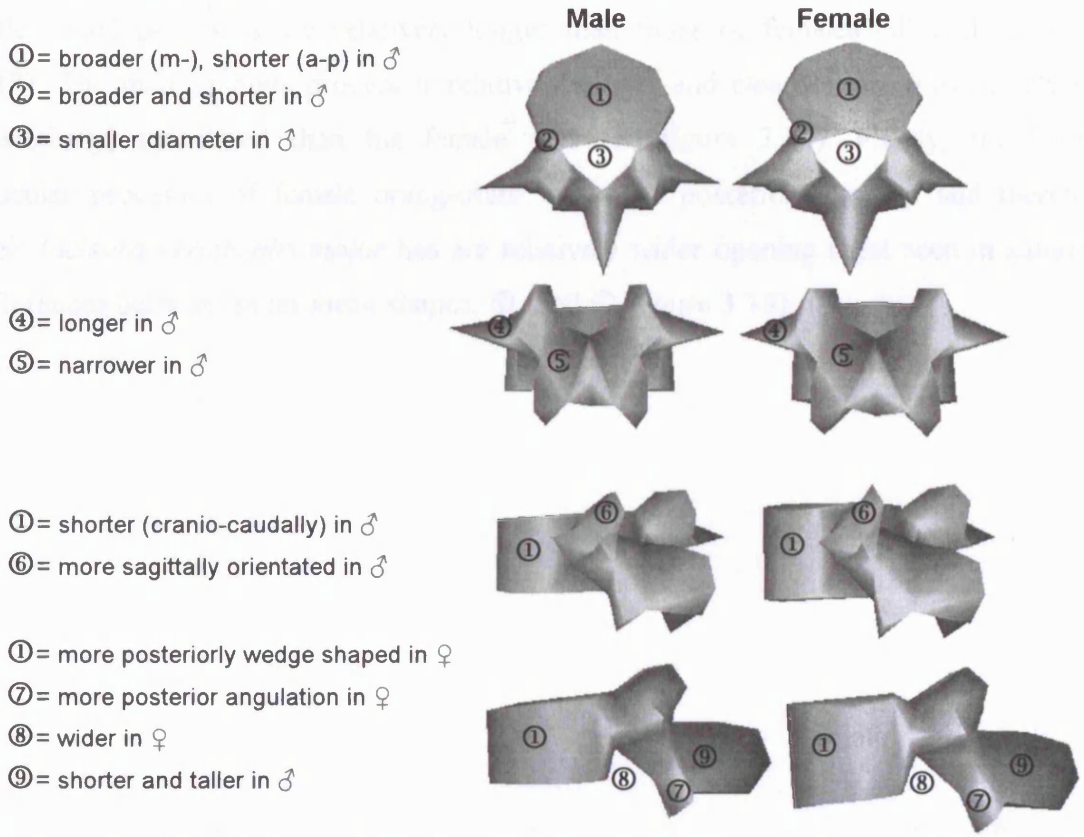


Figure 3.14 Sexual dimorphism in mean vertebral shape of *Homo sapiens*. Female shape: reference shape, male shape: target shape. All differences in shape are relative between sexes. From top to bottom: superior, posterior, left postero-lateral, and left lateral views. ① = vertebral body ② = pedicles ③ = vertebral foramen ④ = costal processes superior articular joint facets ⑤ = vertebral arch ⑥ = superior articular processes ⑦ = inferior articular processes ⑧ = *Incisura vertebralis major* ⑨= spinous process

Pongo pygmaeus

Figures 3.15 to 3.17 and 3.18 illustrate intra-specific differences in shape between the sexes of *Pongo pygmaeus*. Only L1 to L3 are presented since it was only possible for these three vertebrae to identify PCs (from PCA/GPA on total samples) with step-wise discriminant analysis which are able to discriminate significantly between the sexes. These results are not based on large sample sizes and are therefore to be approached cautiously when later interpreted. Sexual dimorphism in *Pongo* vertebral shapes follows a pattern already observed in *Gorilla* and *Homo sapiens*. Thus, the most obvious differences in shape between the sexes are observed in the dimensions of the vertebral bodies. Male orang-utans have relatively shorter, in medio-lateral dimensions relatively broader, and in antero-posterior direction relatively shorter vertebral bodies (①, figure 3.18). They are also more anteriorly wedge shaped than their female counterparts. Male pedicles are, as in *Gorilla* and *Homo sapiens*, relatively broader and shorter than those of females and in consequence, the male vertebral foramen is relatively smaller than the female one (② and ③, figure 3.18). Male vertebral arches are relatively narrower and male costal processes are relatively longer than those of females (④ and ⑤, figure 3.18). The male spinous process is relatively longer and clearly more horizontally (i.e. posteriorly) orientated than the female one (⑧, figure 3.18). Finally, the inferior articular processes of female orang-utans are more posteriorly angled and therefore, their *Incisura vertebralis major* has are relatively wider opening (best seen in summary differences between sexes mean shapes, ⑥, and ⑦, figure 3.18).

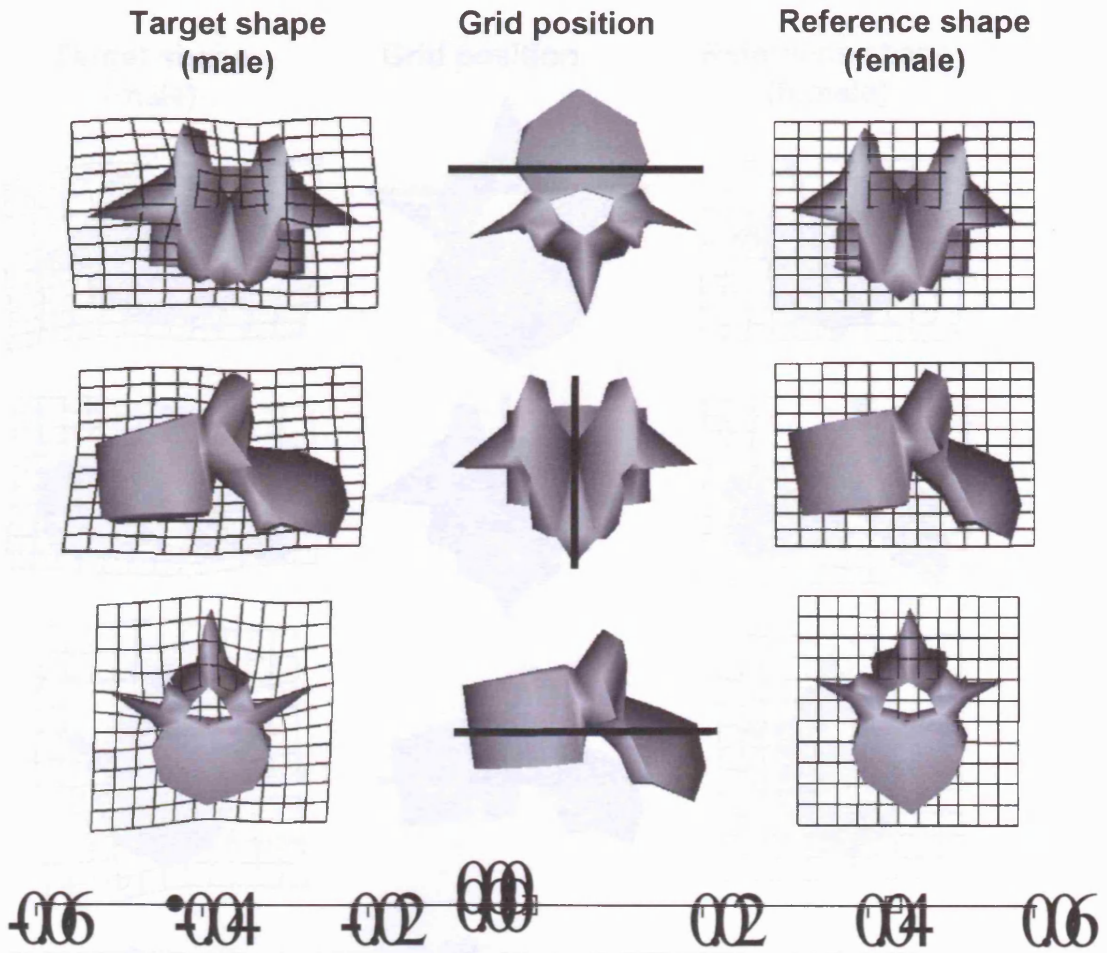


Figure 3.15 Sexual dimorphism in mean lumbar vertebral shape (L1), *Pongo pygmaeus*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

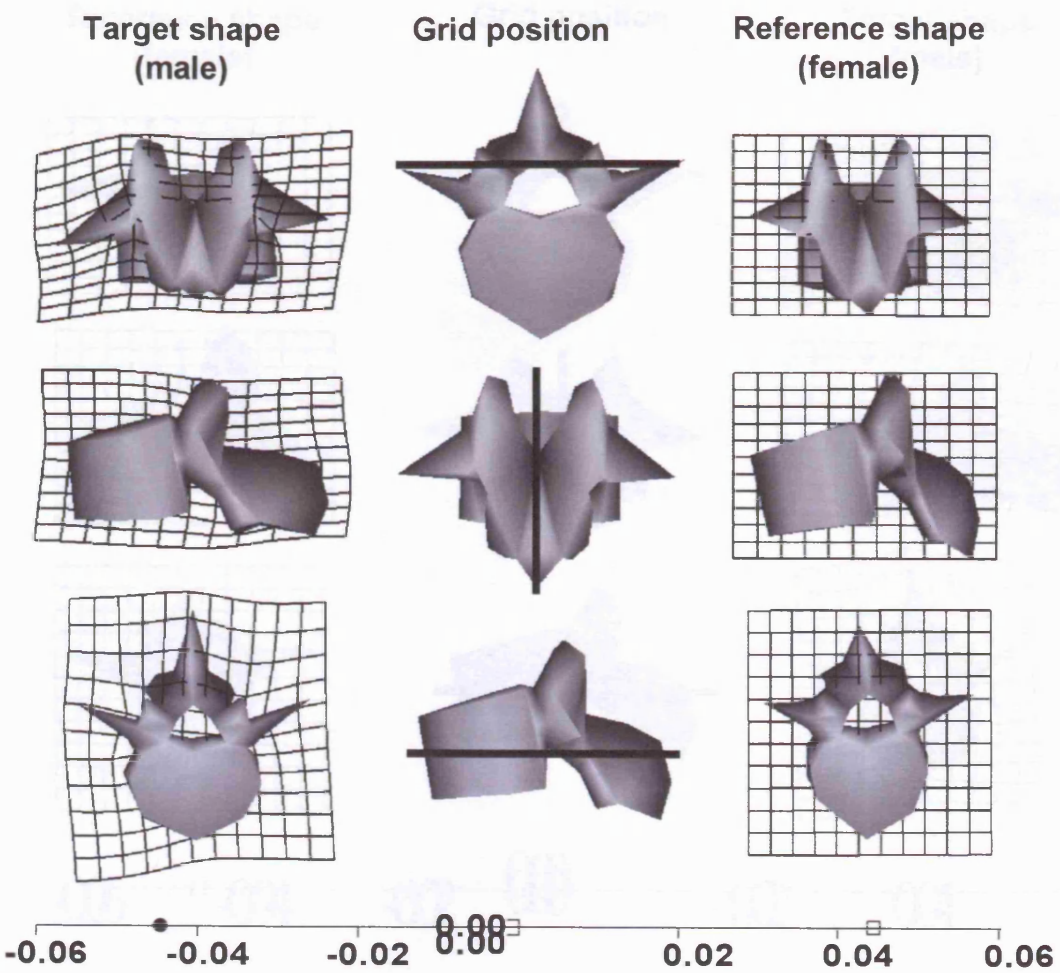


Figure 3.16 Sexual dimorphism in mean lumbar vertebral shape (L2), *Pongo pygmaeus*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

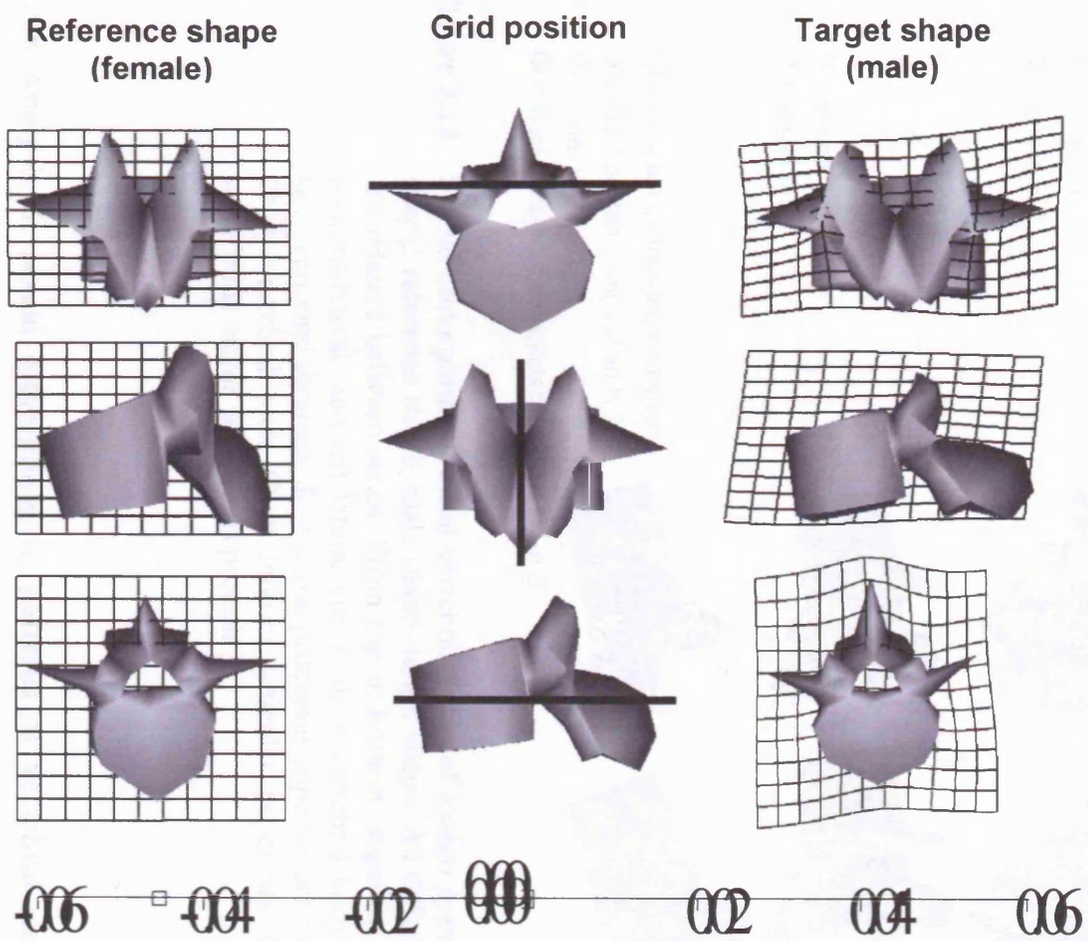


Figure 3.17 Sexual dimorphism in mean lumbar vertebral shape (L3), *Pongo pygmaeus*. Posterior, left lateral and superior views (top to bottom). Grid positions indicates positions of greatest grid distortion. Reference shape: □ = female, target shape: ● = male

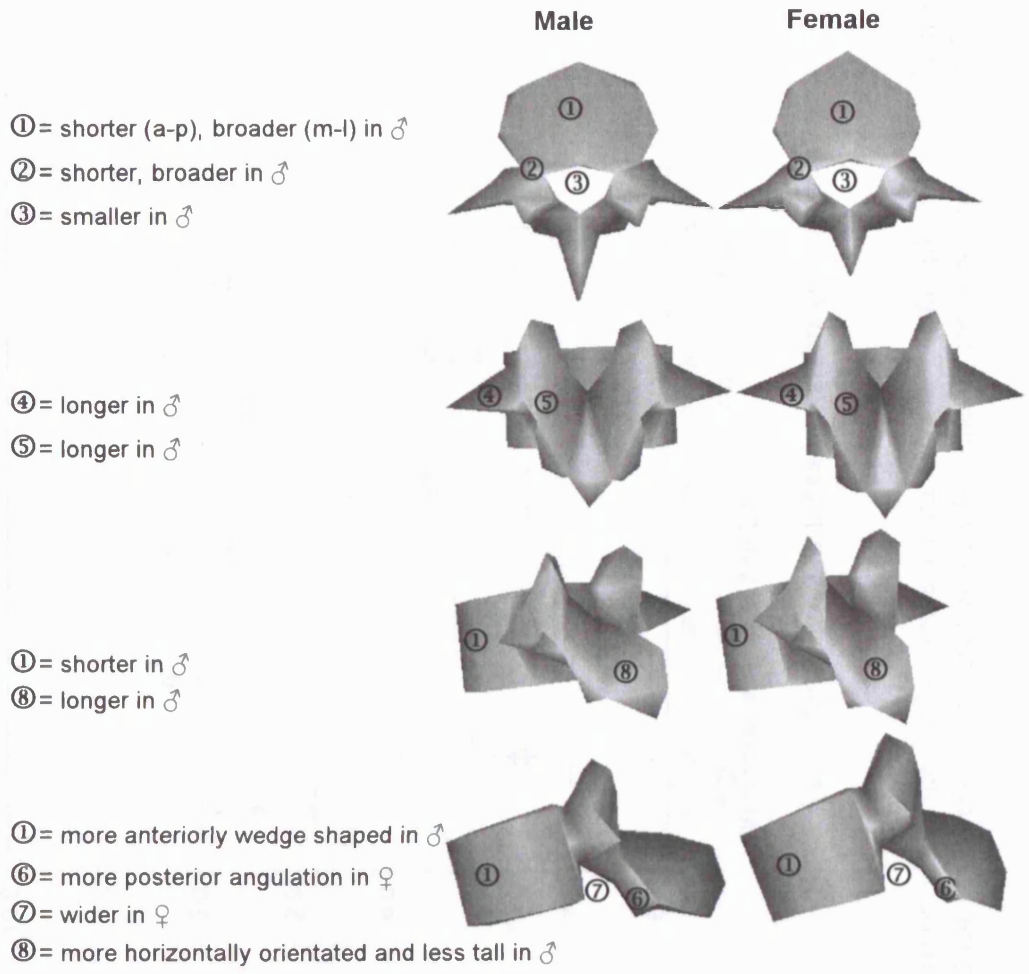
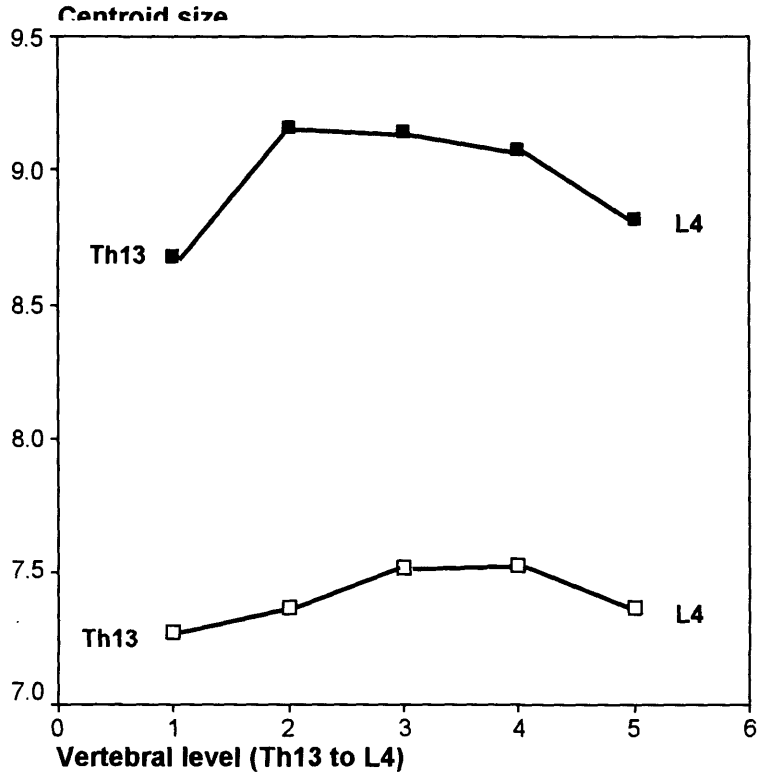


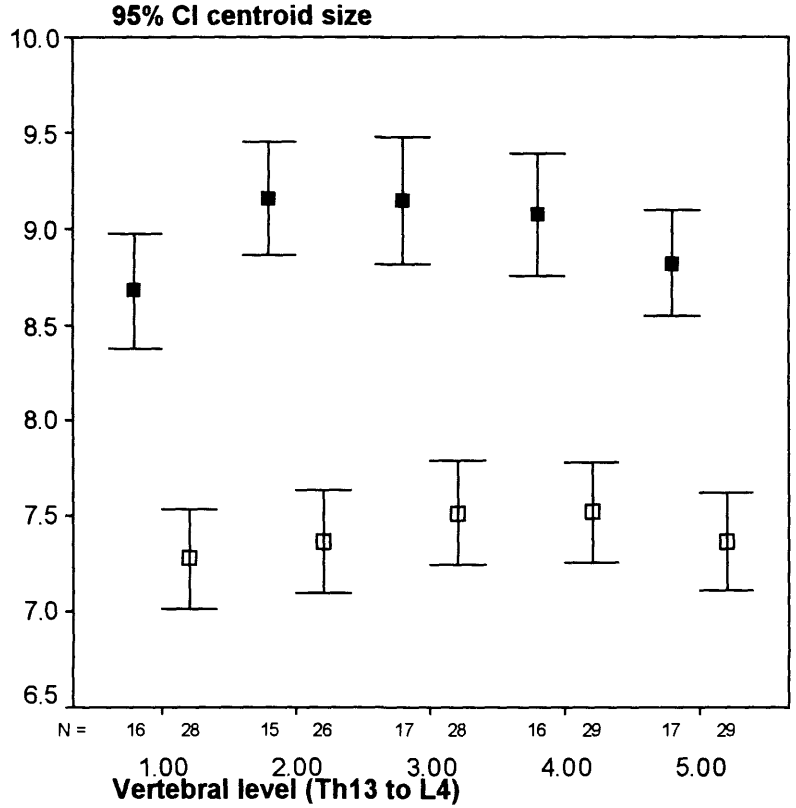
Figure 3.18 Sexual dimorphism in mean vertebral shape of *Pongo pygmaeus*. Female shape: reference shape, male shape: target shape. All differences in shape are relative between sexes. From top to bottom: superior, posterior, left postero-lateral, and left lateral views. ① = vertebral body ② = pedicles ③ = vertebral foramen ④ = costal processes superior articular joint facets ⑤ = vertebral arch ⑥ = inferior articular processes ⑦ = *Incisura vertebralis major* ⑧ spinous process

3.5.5 Analysis 5: sexual dimorphism in patterns of vertebral size and shape variation along the lumbar spine

In contrast to analyses 1 to 4 where shape configurations of single lumbar vertebrae were analysed, analysis 5 explores patterns of vertebral size and shape variation along the lumbar spine and potential sexual dimorphism thereof. Within each taxon, patterns of size and shape variation along the lumbar spine are visualized for both males and females. In the case of size variation patterns, mean centroid size was calculated for each lumbar vertebra and each sex. Scatter plots of centroid size (y-axis) versus vertebral levels (x-axis) in two dimensions are displayed.

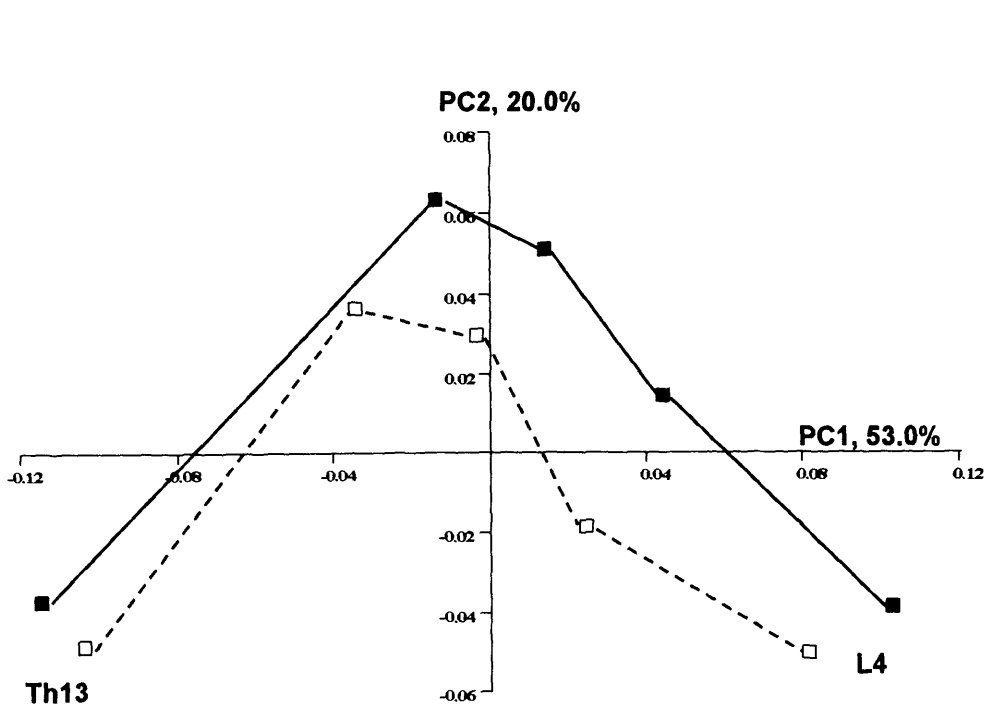


A: Patterns of vertebral size variation (mean vertebral shapes)



B: 95% confidence intervals for each vertebra (full samples)

Figure 3.19 Sexual dimorphism in patterns of mean vertebral size variation along the lumbar spine within *Gorilla gorilla* **(A)** 95% confidence interval, vertebral size at each vertebral level **(B)** Th13 and L4 are labelled. Consecutive vertebral means are connected by lines. Full sample n = 279; □ = adult females, ■ = adult males



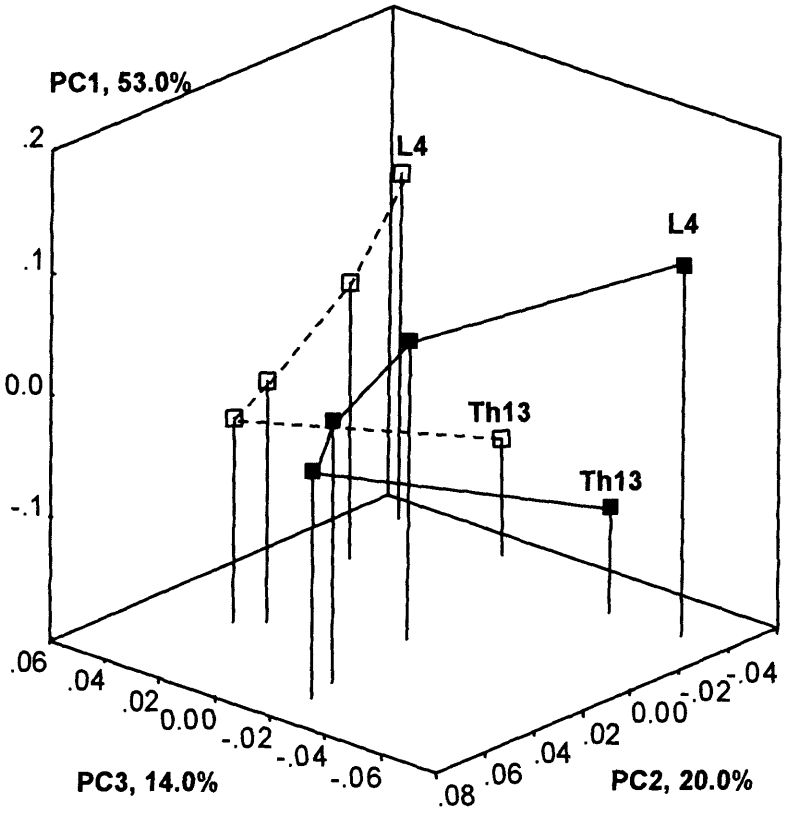
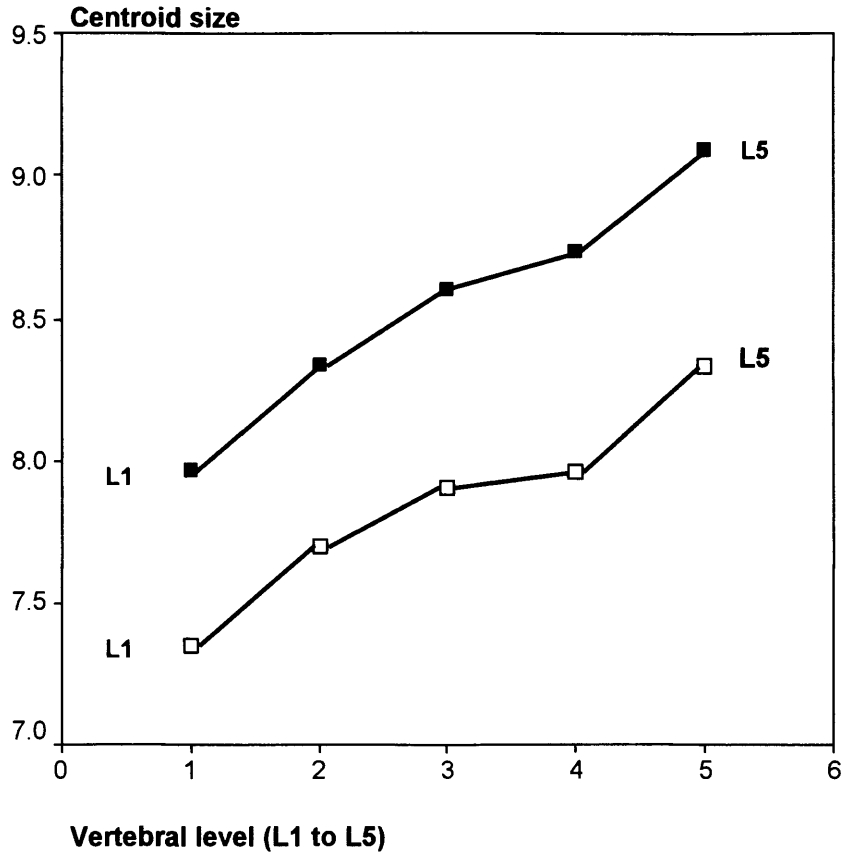
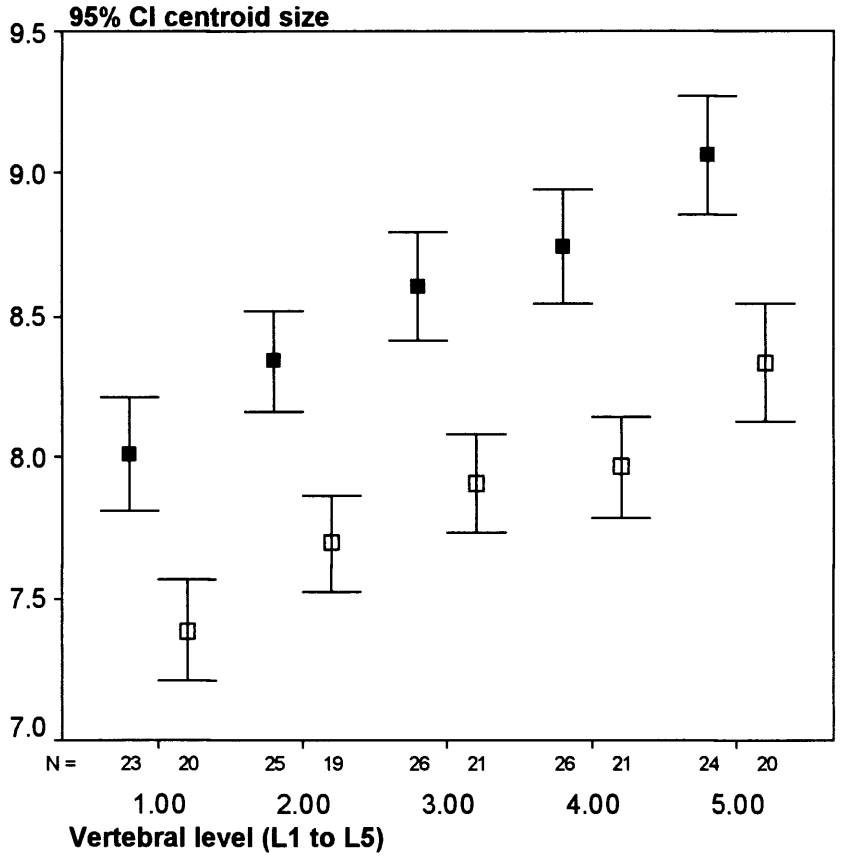


Figure 3.20 Scatter plots in 2 and 3 dimensions, sexual dimorphism in patterns of vertebral shape variation, *Gorilla gorilla*. Consecutive vertebral means are connected by lines to visualize shape variation along the lumbar spine□ = females, ■ = males

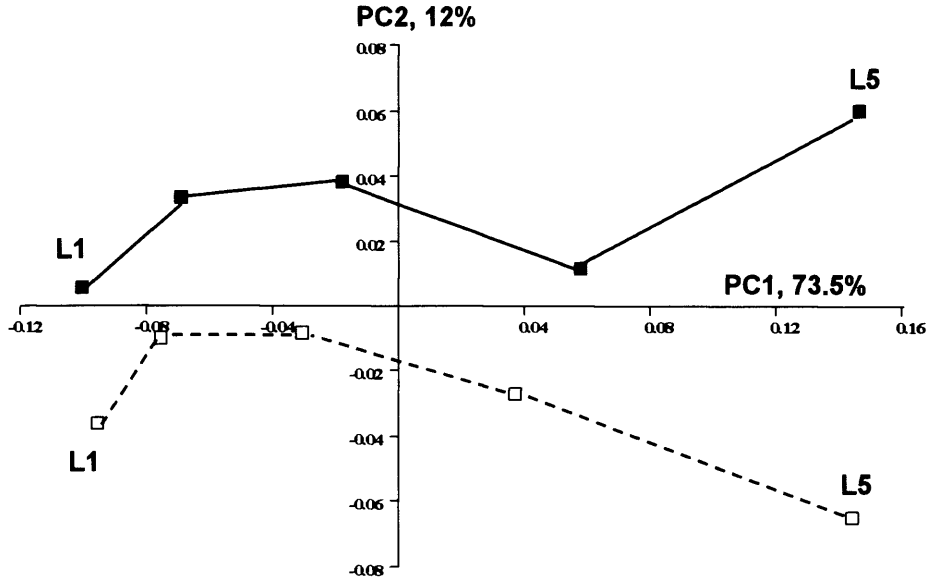


A: Patterns of vertebral size variation (mean vertebral shapes)



B: 95% confidence intervals for each vertebra (full samples)

Figure 3.21 Sexual dimorphism in patterns of mean vertebral size variation along the lumbar spine within *Homo sapiens* **(A)** 95% confidence interval, vertebral size at each vertebral level **(B)** L1 and L5 are labelled. Consecutive vertebrae are connected by lines. Full sample n = 225; □ = adult females, ■ = adult males



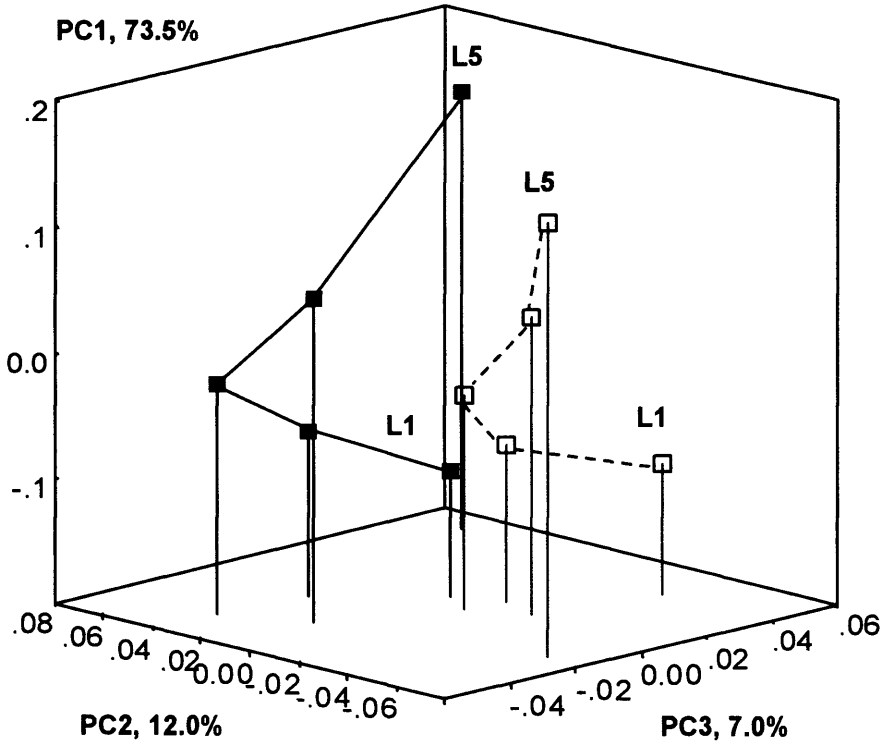
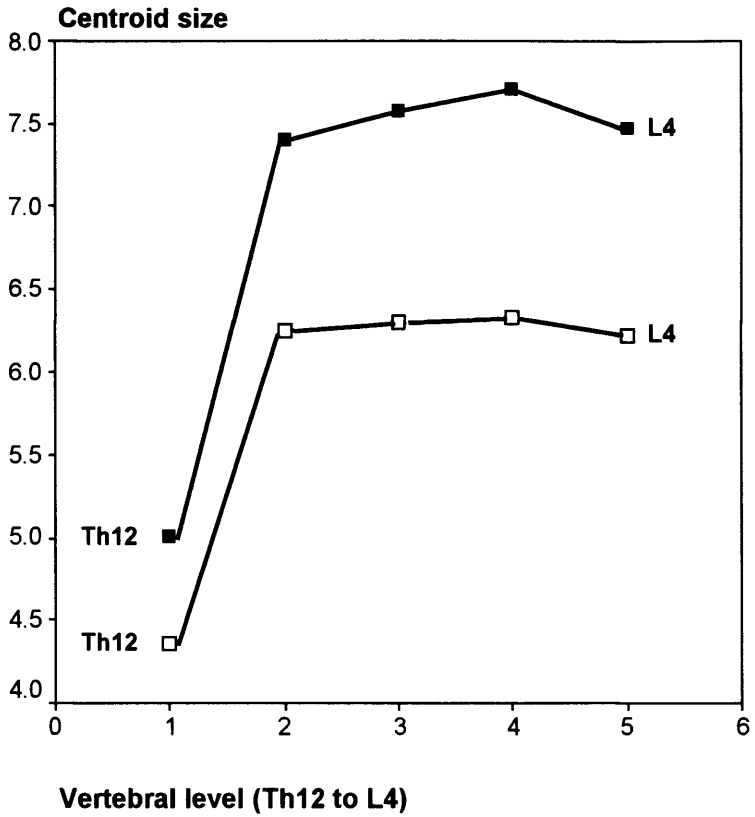
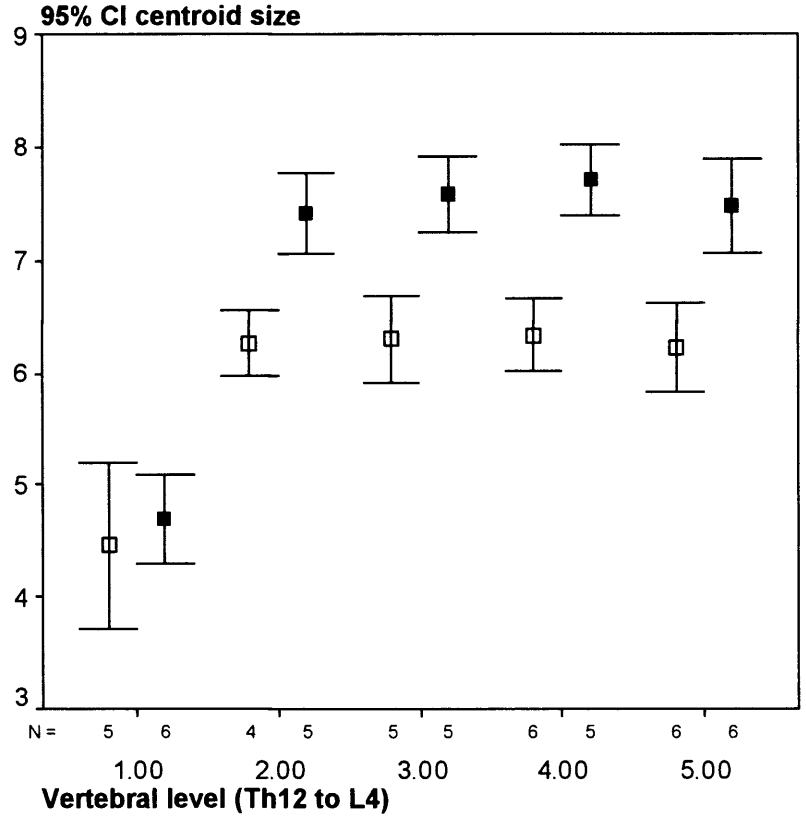


Figure 3.22 Scatter plots in 2 and 3 dimensions, sexual dimorphism in patterns of vertebral shape variation, *Homo sapiens*. Consecutive vertebrae are connected by lines to visualize shape variation along the lumbar spine □ = females, ■ = males

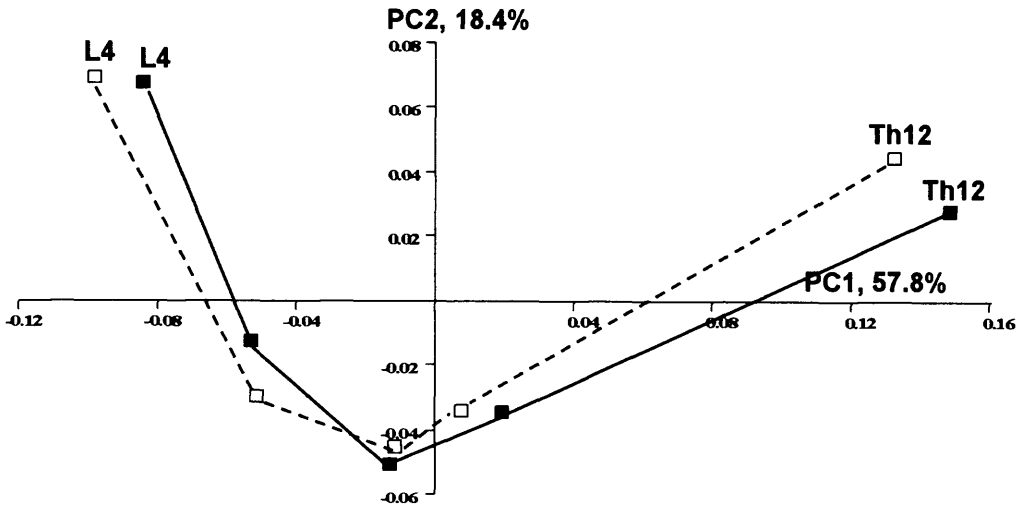




A: Patterns of vertebral size variation (mean vertebral shapes)

B: 95% confidence intervals for each vertebra (full samples)

Figure 3.23 Sexual dimorphism in patterns of mean vertebral size variation along the lumbar spine within *Pongo pygmaeus* **(A)** 95% confidence interval, vertebral size at each vertebral level **(B)** Th12 and L4 are labelled. Consecutive vertebrae are connected by lines. Full sample n = 54; □ = adult females, ■ = adult males



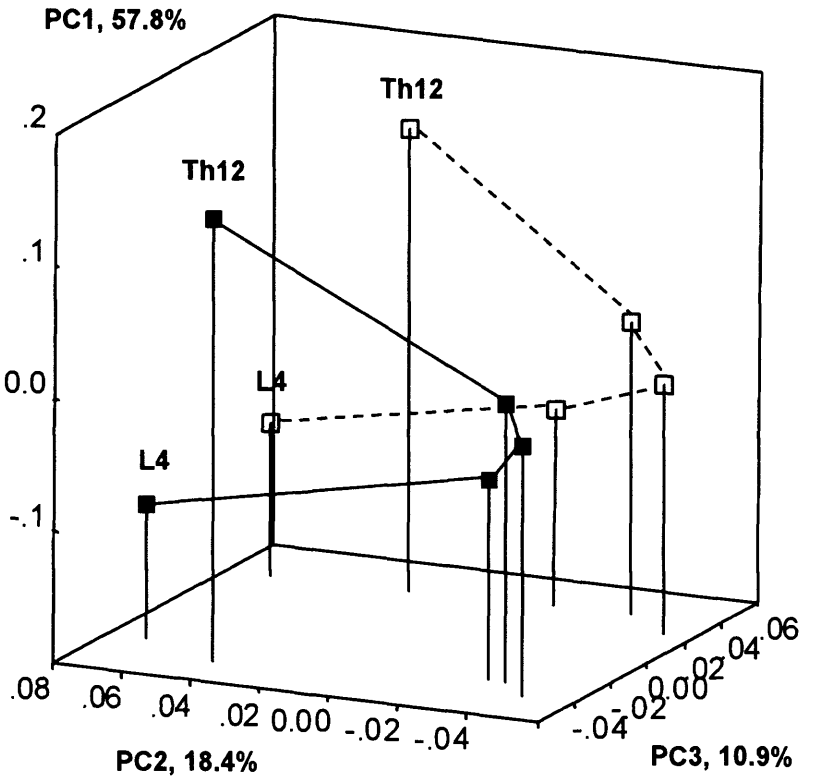
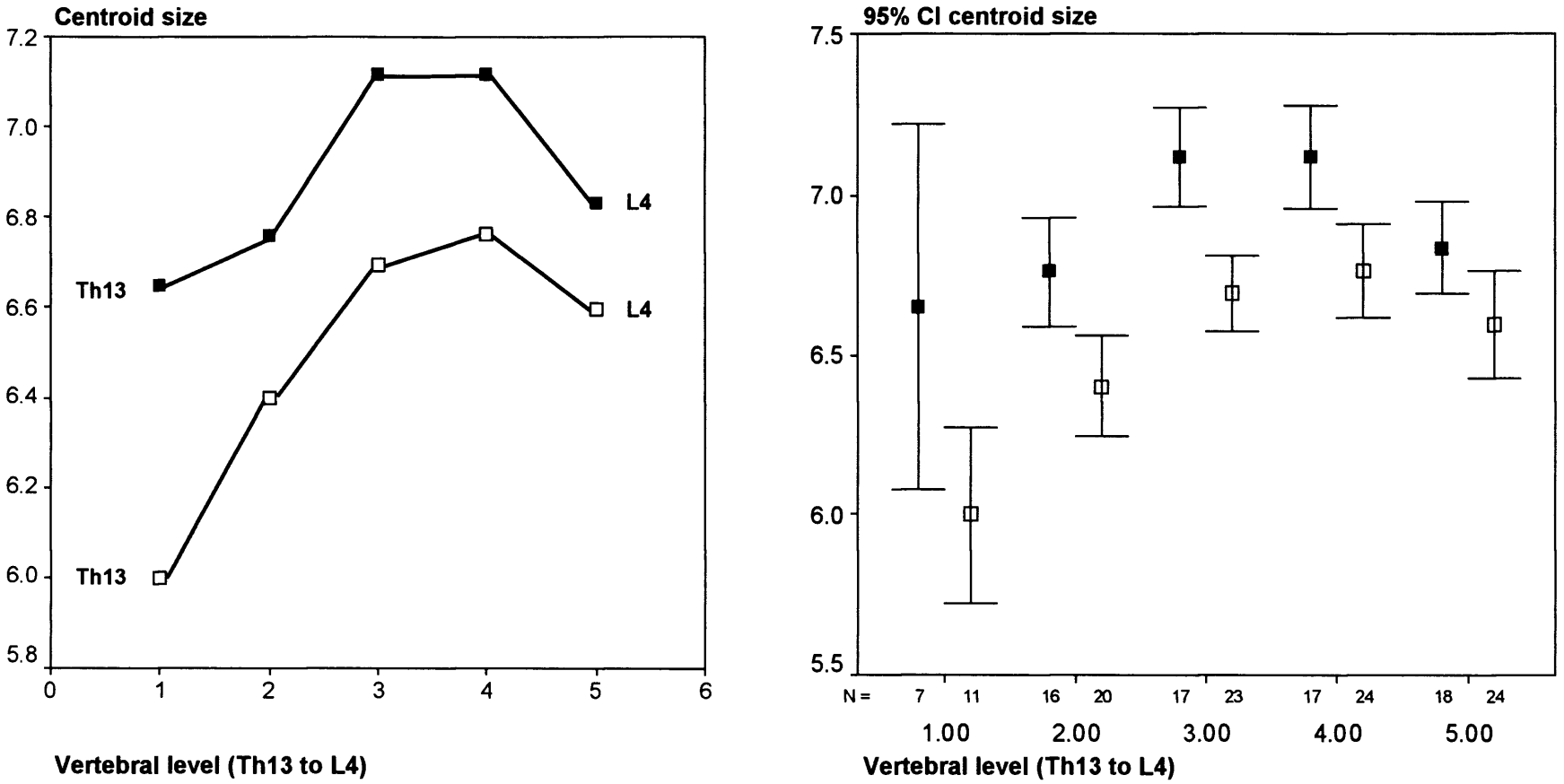


Figure 3.24 Scatter plots in 2 and 3 dimensions, sexual dimorphism in patterns of vertebral shape variation *Pongo pygmaeus*. Consecutive vertebrae are connected by lines to visualize shape variation along the lumbar spine. Th12 and L4 are labelled □ = females, ■ = males.



A: Patte

Figure 3.25 Sexual dimorphism in patterns of mean vertebral size variation along the lumbar spine within *Pan troglodytes* **(A)** 95% confidence interval, vertebral size at each vertebral level **(B)** Th13 and L4 are labelled. Consecutive vertebrae are connected by lines. Full sample n = 202; □ = adult females, ■ = adult males

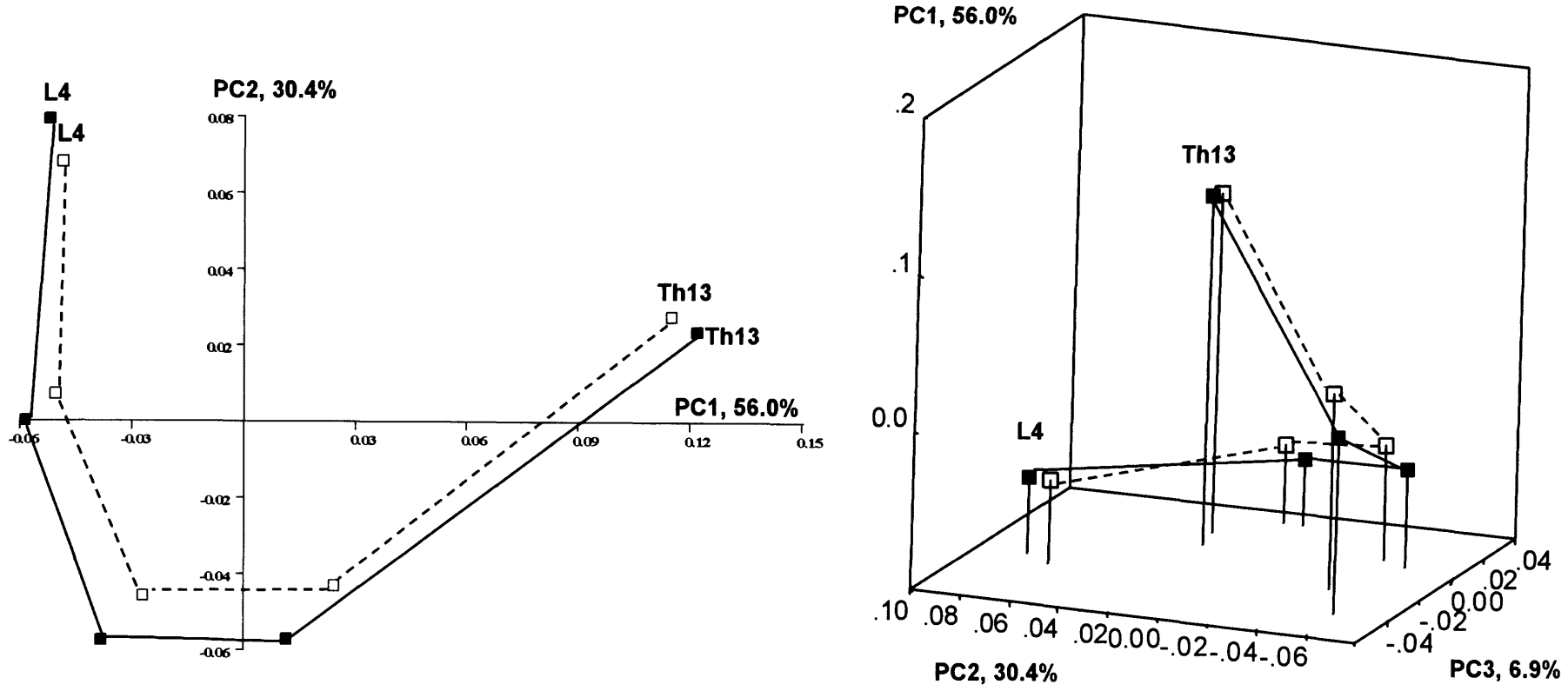


Figure 3.26 Scatter plots in 2 and 3 dimensions, sexual dimorphism in patterns of vertebral shape variation *Pan troglodytes.* Consecutive vertebrae are connected by lines to visualize shape variation along the lumbar spine. □ = females, ■ = males

To better visualize decreases and increases in vertebral size between consecutive vertebrae, they have been connected with lines. In addition, the same plots showing the 95% confidence interval (CI) for vertebral mean sizes are presented. Patterns of shape variation along the lumbar spine and sexual dimorphism between patterns are displayed in two- and three-dimensional scatter plots. These plots are produced by analysing mean shape data of each lumbar vertebra with GPA/PCA for both sexes of each taxon. As in the case of size, shape variations between consecutive mean shapes are represented by connecting lines. Results are presented separately for each taxon.

Gorilla gorilla

Both patterns of vertebral size and shape variation along the lumbar spine of male and female *Gorilla* are quite similar to each other (see figures 3.19, size and 3.20, shape). Generally, the *Gorilla* size variation pattern shows size increase from Th13 towards the midsection of the lumbar spine, which is followed by a decrease in vertebral size towards the last lumbar. In the shape variation pattern a noticeable "jump" in shape differences is observed – not surprisingly – between Th13 and L1.

Homo sapiens

Patterns of vertebral size variation along the lumbar spine are similar for male and female *Homo sapiens* (see figure 3.21). In both, vertebral size increases steadily from L1 to L5. The increase in vertebral size between consecutive vertebrae is largest between L4 and L5. In contrast, the patterns of vertebral shape variation along the lumbar spine are not identical between female and male *Homo sapiens* (see figure 3.22). The patterns are similar from L1 to L4 but diverge visibly between L4 to L5. Nevertheless, in both sexes, differences in shape between pairs of neighbouring vertebrae increase steadily from L1 to L5 and are largest between L4 and L5 (see figure 3.22).

Pongo pygmaeus

The vertebral size variation patterns of male and female *Pongo* are not as similar to each other as was the case in *Gorilla* (see figure 3.23). However, the overall patterns of males and females are the same and resemble those of *Gorilla*. Nevertheless, the differences in vertebral size variation patterns between the sexes highly likely is an artefact caused by the small *Pongo* samples available and therefore of no particular consequence. The relatively extensive 95% confidence intervals observed in *Pongo* corroborate this

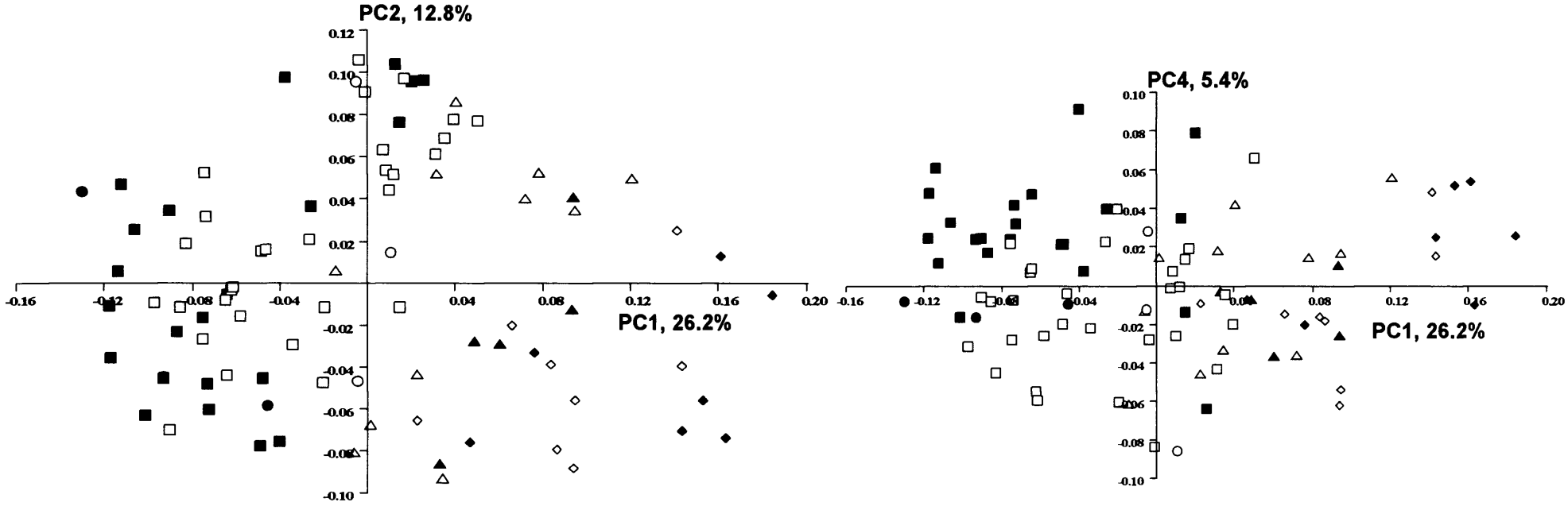
assumption (figure 3.23B). The patterns of vertebral shape variation of male and female *Pongo* are very similar to each other (figure 3.24).

Pan troglodytes

Both patterns of vertebral size and shape variation of male and female *Pan* are similar to each other (figures 3.25, and 3.26). In the patterns of size variation, a sharp increase in vertebral size is observed from Th13 to L1 followed by another (smaller) increase in vertebral size from L1 to L2. From L2 to L4, vertebral size steadily decreases. The patterns of vertebral shape variation resembles those observed in *Gorilla* and *Pan*: larger rates of shape variation are observed between Th13 and L1 and L3 and L4.

3.5.6 Analysis 6: the postnatal development of sexual dimorphism in vertebral size and shape

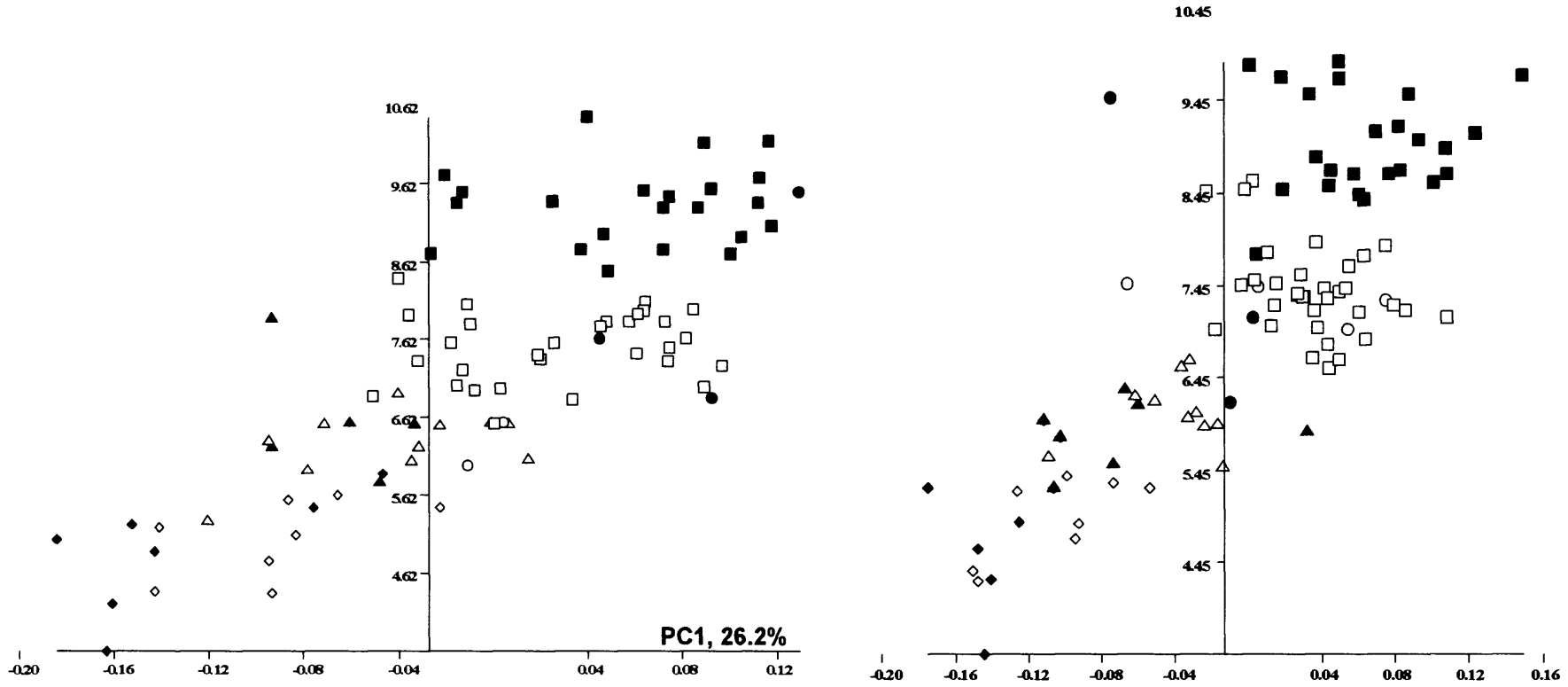
To assess the trajectories, along which female and male infant vertebral sizes and shapes transform towards adult size and shapes, GPA/PCA analysis was performed on samples of each taxon consisting of different age groups (labelled as infant, juvenile, subadult, and adult, for a definition of these groups, see Chapter II, pp. 93-95). The analyses are performed at each vertebral comparison level to check if the patterns of size and shape variation between age groups (growth trajectories) are the same for each individual vertebra. Also, the analysis of total samples (all vertebrae at once) usually produced too large an overlap of individuals along the axis of the growth trajectories and it became difficult to see differences between the sexes. Step-wise discriminant analysis was again used to identify any PC that summarizes differences in vertebral shape between the sexes. In order to prevent endless repetitions, plots of PCs are shown for the first and last lumbar vertebrae of each taxon only. Results for vertebrae L2 and L3 (and in the case of modern humans L4) were always highly similar to the ones of the first and last lumbars. Results are presented separately for each taxon.



A: PC1 vs. PC2, level L1

B: PC1 vs. PC4, level L1

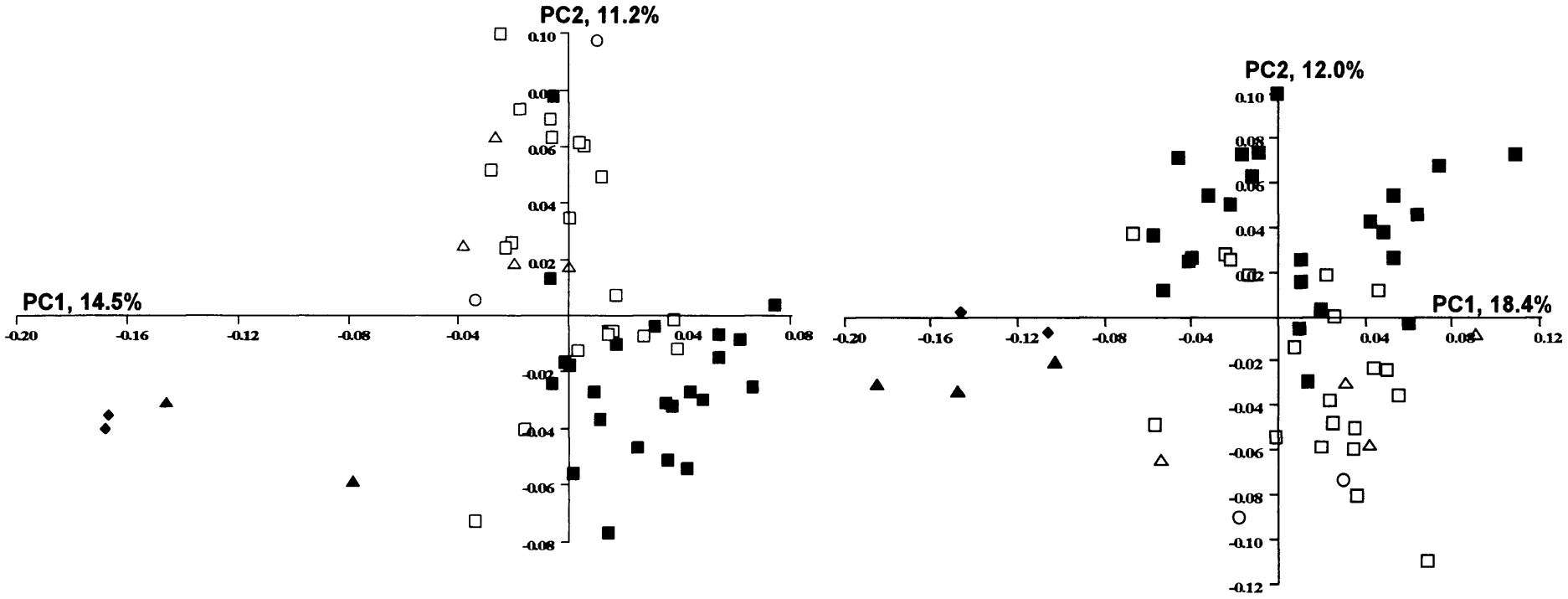
Figure 3.27 Scatter plots of PC1 vs. PC2 **(A)** and PC1 vs. PC4 **(B)**, extracted from full *Gorilla gorilla* sample analysis at comparison level L1. Sample contains infants, juveniles, sub-adults and adult specimens ◆ = male infant, ◇ = female infant, ▲= male juvenile, △ = female juvenile, ● = male subadult, ○ = female subadult, ■ = adult male, □ = adult female



A: comparison level L1

B: Comparison level L4

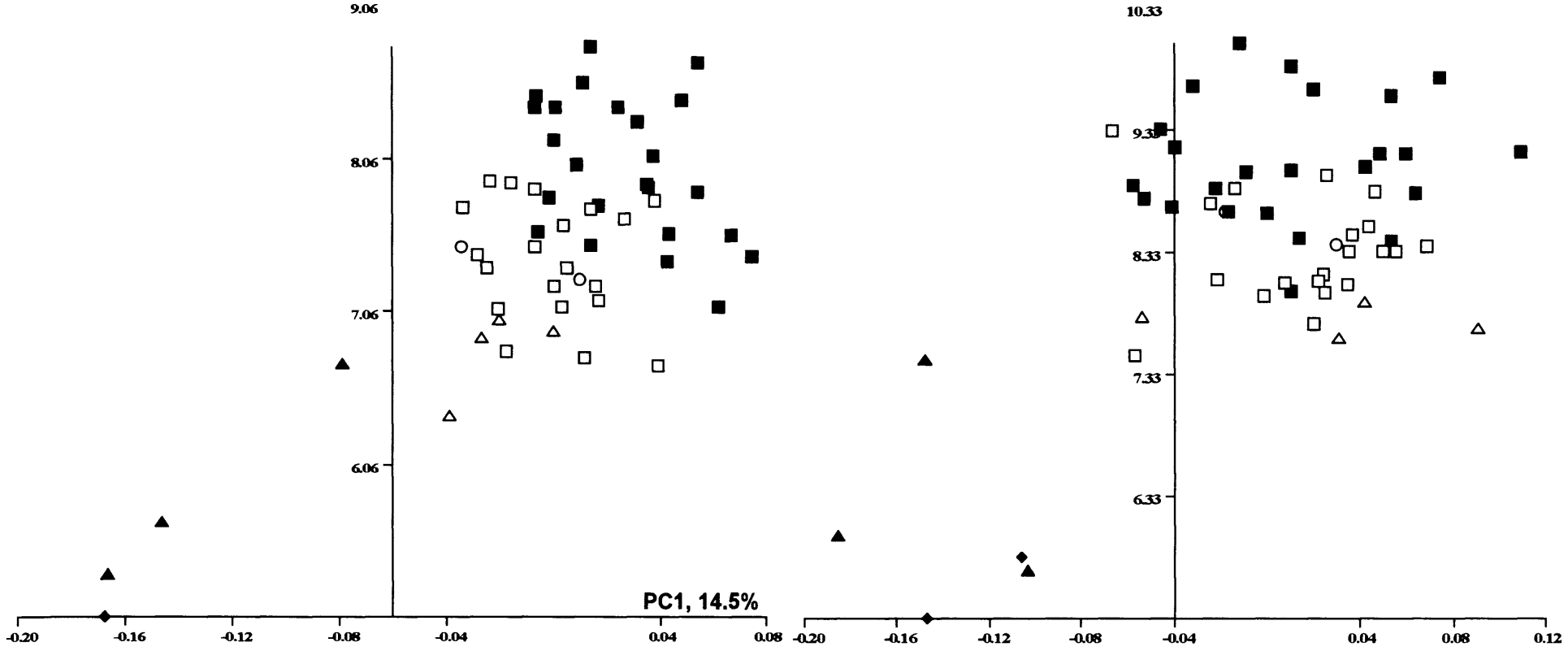
Figure 3.28 Scatter plots of PC1 vs. centroid size at level L1 **(A)** and level L4 **(B)**, extracted from full *Gorilla gorilla* sample analysis. They represent male and female trajectories of vertebral size and shape variation from infants to adults. Full samples contain different age groups (infant, juvenile, subadult, and adult) ◆ = male infant, ◇ = female infant, ▲= male juvenile, △ = female juvenile, ● = male subadult, ○ = female subadult, ■ = adult male, □ = adult female



A: PC1 vs. PC2, level L1

B: PC1 vs. PC2 level L5

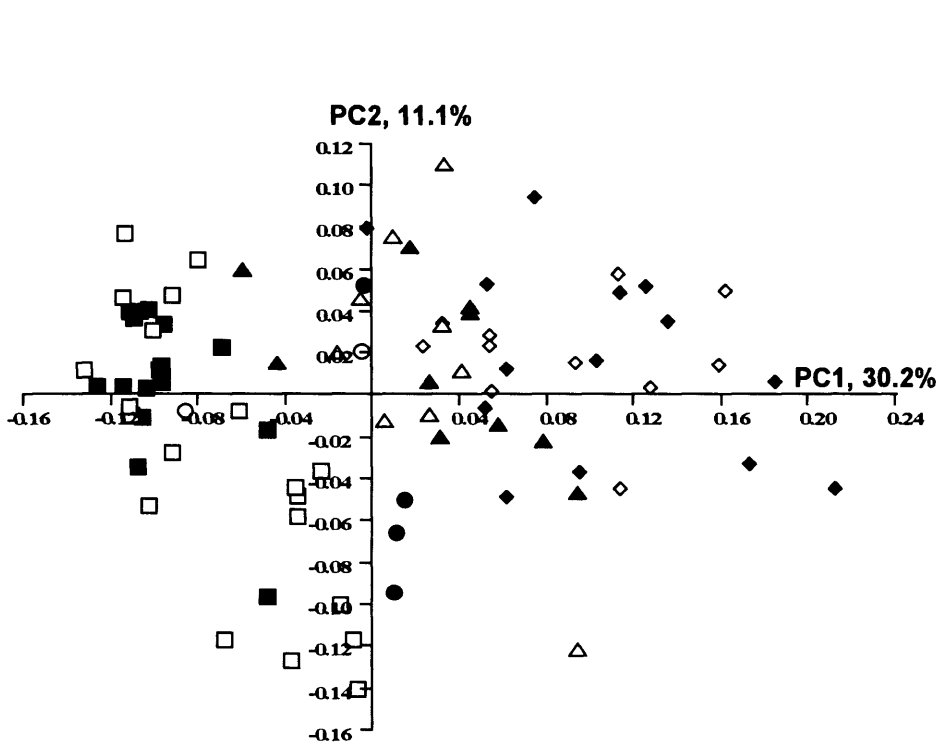
Figure 3.29 Scatter plots of PC1 vs. PC2, level L1 **(A)** and PC1 vs. PC2, level L5 **(B)**, extracted from full *Homo sapiens* sample analysis. Sample contains infants, juveniles, sub-adults and adult specimens ◆ = male infant, ▲ = male juvenile, △ = female juvenile, ○ = female subadult, ■ = adult male, □ = adult female



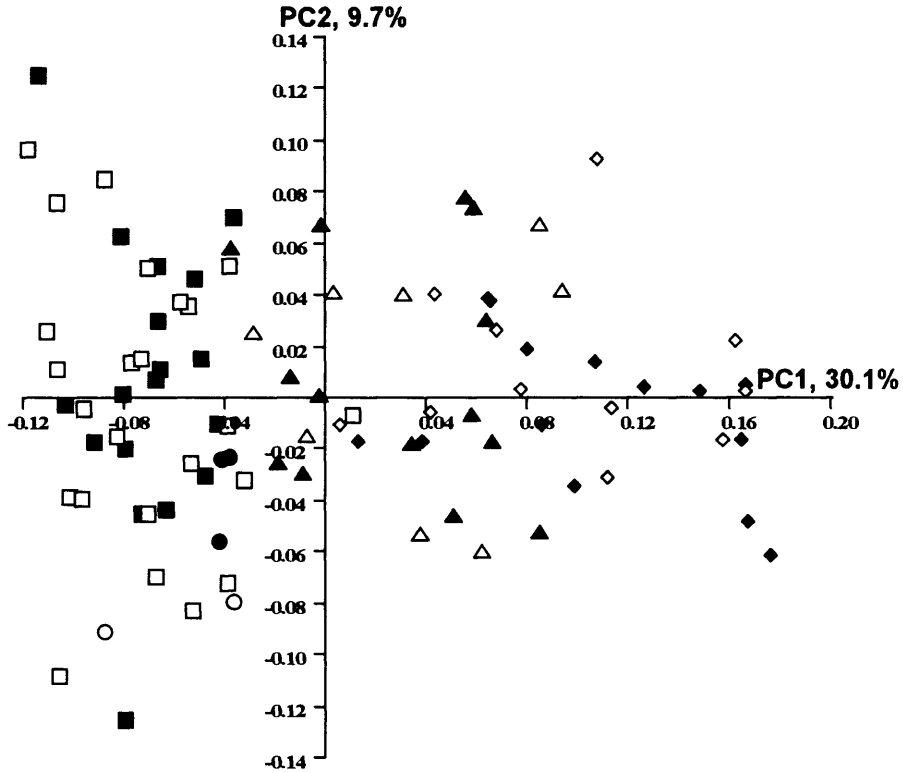
A: Comparison level L1

B: Comparison level L5

Figure 3.30 Scatters plot of PC1 vs. centroid size at level L1 **(A)** and level L5 **(B)**, extracted from full *Homo sapiens* sample analysis. They represent male and female trajectories of vertebral size and shape variation from infants to adults. Full samples contain different age groups (infant, juvenile, subadult, and adult). ◆ = male infant, ▲= male juvenile, △ = female juvenile, ○ = female subadult, ■ = adult male, □ = adult female

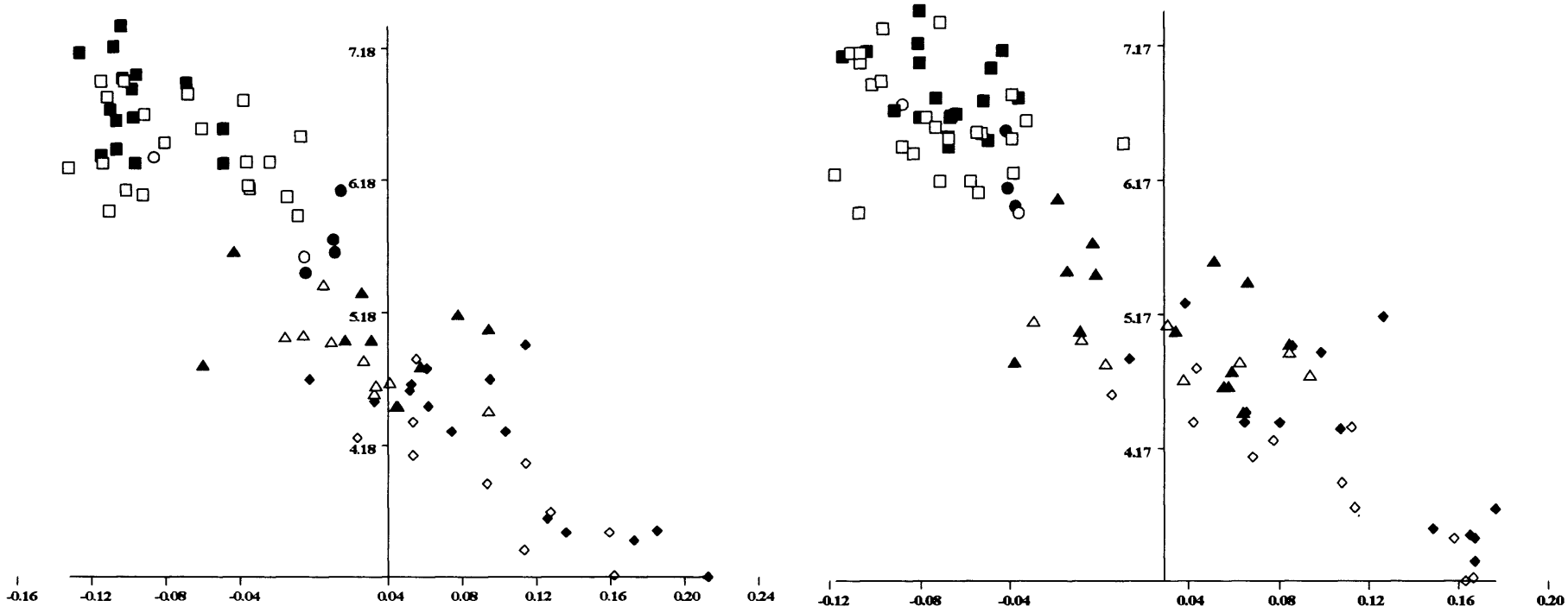


A: PC1 vs. PC2, level L1



B: PC1 vs. PC2 level L4

Figure 3.31 Scatter plots of PC1 vs. PC2, level L1 **(A)** and PC1 vs. PC2, level L4 **(B)**, extracted from full *Pan troglodytes* sample analysis. Sample contains infants, juveniles, sub-adults and adult specimens ◆ = male infant, ◇ = female infants, ▲ = male juvenile, △ = female juvenile, ● = male subadult, ○ = female subadult, ■ = adult male, □ = adult female



A: Comparison level L1

B: Comparison level L4

Figure 3.32 Scatter plots of PC1 vs. centroid size at level L1 **(A)** and level L4 **(B)**, extracted from full *Pan troglodytes* sample analysis. They represent male and female trajectories of vertebral size and shape variation from infants to adults. Full samples contain different age groups (infant, juvenile, subadult, and adult) ◆ = male infant, ◇ = female infant, ▲= male juvenile, △ = female juvenile, ● = male subadult, ○ = female subadult, ■ = adult male, □ = adult female

Gorilla gorilla

Intra-specific differences in lumbar vertebral size and shape between age groups and sexes of *Gorilla* are presented in figures 3.27 and 3.28. Figure 3.27A shows a scatter plot of PC1 versus PC2, whereas figure 3.27B represents the scatter plot of PC1 versus the strongest sex discriminator (PC4 in this case) at comparison level 1. Differences in vertebral shape between age groups are substantial and are principally summarized by PC 1 (figure 3.27A, B). When morphing the shape configurations along the axis of PC2, this visual inspection shows that the relatively large proportion of total shape variation summarized by PC2, (= 12.8%) reflects the more the 'thoracic' than 'lumbar' shape of some individuals. Step-wise discriminant analysis identified PC4 (= 5.4%) as the strongest discriminator between the sexes (see figure 3.27B). However, at comparison level 4 (last lumbars), step-wise discriminant analysis failed to identify a significant sex discriminating PC (no plots shown). The relatively large degree of shape variation within the adult sample (summarized mainly by PC2, figure 3.27A) is related to different degrees of sacralization of the last lumbar vertebra within the adult sample. Shape variation related to degrees of sacralization is exclusively observed within the adult sample. To see how *Gorilla* male and female vertebral shapes vary with size, plots of PC1 (which is the PC that summarizes most size related shape variation in each analysis) versus centroid size at comparison levels L1 and L4 are presented in figure 3.28. These plots show that at each level, males extend their vertebral size into larger size ranges than females. In addition, although females and males principally scale along PC1 at the same rate, males show a larger rate of size increase relative to PC1 shape (summarising age related shape changes such as elongation of the vertebral processes, elongating and widening of the vertebral body etc.) as they approach adulthood.

Homo sapiens

Scatter plots of PC1 versus PC2 at comparison levels 1 an 5 from an analysis of the age series of *Homo sapiens* are presented in 3.29. Male and female adults are more distinctly separated than were *Gorilla* adults. The plots in figures 3.30A and B indicate a potential different data distribution for immature male and female human specimens. Yet no adequate subadult human sample was available to explore whether the plots shown in figure 3.29 reflect a different data distributions for the entire male and female human samples (including subadult age groups) or if this is an artefact of the small immature samples. Further data would be needed to investigate this. Figure 3.30 shows

scatter plots of PC1 vs. centroid size for L1 and L5 of modern humans. At level L1 (figure 3.30A), males slightly extend their vertebral size into larger size ranges than females. At level L5 a slight separation between the scaling of males and females along PC1 is observed (see figure 3.30B).

Pongo pygmaeus

The *Pongo* sample was deemed too small to extract any PC scatter plots which could be explored with success.

Pan troglodytes

Intra-specific differences in lumbar vertebral size and shape between age groups and sexes of *Pan* are presented in figures 3.31. It shows scatter plots of PC1 versus PC2 at comparison level L1, and level L4 respectively. In both cases, PC2 was identified as the strongest discriminator between the sexes by stepwise discriminant analysis. Nevertheless, at both comparison levels, the discrimination between the sexes along the axes of PC2 (see figure 3.31A and B) is very weak. Figure 3.32 shows scatter plots of PC1 versus centroid size at comparison levels L1 and L4 (figures 3.32A and B) for full age and sex samples of *Pan*. Female and male trajectories are virtually the same. In contrast to the large sized male apes (*Gorilla* and *Pongo*), there is no evidence of sexual dimorphism.

3.6 Discussion

This study has examined sexual dimorphism in vertebral morphology (size and shape) within hominoid taxa. The aim has been to examine the extent to which such differences reflect differences in body weight and - where these fail to explain sexual dimorphism in vertebral morphology – differences in locomotor repertoires. This study (together with that in the next chapter, examining inter-specific differences in vertebral morphology between hominoid taxa) serves as an important preliminary to the penultimate chapter in which the vertebral morphology of some fossil taxa is compared with that of living hominoids. They provide the background against which differences between fossils and extant species can be evaluated.

The work of this chapter has focused on characterising the extent of sexual dimorphism within the lumbar column of extant hominoids and in trying to relate dimorphism to

pertinent factors. Thus it is a reasonable first assumption that dimorphism in body weight and locomotion impact on vertebral morphology. To date, there is no knowledge of the relative contribution of these factors to differences between spinal regions, individual vertebrae or vertebral elements such as the body or arch. The analyses of this chapter aim to tease out the effects of these potential influences through comparative studies of individual vertebrae and of patterns of inter-segmental variation in size and shape within each taxon.

The specific aims are summarized as follows:

1. To confirm that sexual dimorphism in lumbar vertebral size and shape exists within *Homo sapiens, Gorilla gorilla, Pan troglodytes*, and *Pongo pygmaeus*

2. Once confirmed, to investigate if these dimorphisms in vertebral size and shape within each taxon are related to dimorphisms in body weight and locomotor repertoires

3. To assess the extent to which the patterns of inter-segmental size and shape variation along the lumbar spine differ between the sexes within the four hominoid taxa in the study

4. To assess how these dimorphisms are established during postnatal ontogeny

The introductory review of the present study shows, that some of the living hominoids display considerable dimorphism in body weight and frequencies of locomotor modes. *Gorilla* and *Pongo* are the most sexually dimorphic taxa with regard to body weight, followed by *Homo sapiens* and *Pan*. Sexual dimorphism in frequencies of locomotor modes is large in *Gorilla* and *Pan*, followed by *Pongo* and humans. Differences in body weight are most likely to impact on the morphology of the vertebral elements that are responsible for weight transmission through the lumbar spine. The impact of sexual dimorphism in locomotor mode frequencies is less clear. However, one might expect it to be manifest in the articular joints and the vertebral processes since these structures are closely related to locomotor function through functions in motion and muscle attachments. Additionally, since locomotion affects the ways in which body weight is transmitted to the substrate (ground or tree), it is likely that locomotor dimorphism (as

well as differences in body mass) will have an impact on weight bearing structures of the spine; anteriorly the bodies and posteriorly the arches and their articulating structures. Further the sizes and shapes of vertebrae are patterned through genetic systems during development.

Hypotheses, addressing the previously summarized aims are organised in five groups. The first three deal with differences between vertebral levels, taken one at a time. The first addresses the presence or absence of sexual dimorphism in vertebral size and shape, the second addresses relationships between vertebral size and shape and sexual dimorphism in body weight, and the third addresses the impact of sexual dimorphism in frequencies of locomotor modes on vertebral size and shape. The fifth hypothesis deals with differences between the sexes in the ways in which the last five presacral vertebrae show inter-segmental patterns of size and shape variation. This discussion is organised according to the study aims.

3.6.1 Does sexual dimorphism in lumbar vertebral size and shape exist within *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*?

Before we can examine the relationship between sexual dimorphism in vertebral size or shape and factors such as sexual dimorphism in body weight and locomotor repertoires, the presence of sexual dimorphism in vertebral size and shape has to be confirmed.

Thus hypotheses 1.1 (differences in vertebral size) and 1.2 (differences in vertebral shape) were formulated. The testing of these simply addresses the questions of presence or absence of sexual dimorphism in vertebral size and shape within each hominoid taxon.

Analysis 1 (addressing questions of hypothesis 1.1) assessed sexual dimorphism in vertebral size at each comparison level and within each taxon by calculating differences in vertebral centroid sizes between the sexes. Levels of significance were estimated by independent t-tests. Results from analysis 1 indicate large sexual dimorphism in vertebral size in *Gorilla* and *Pongo*. Differences in vertebral size were smallest between the sexes in *Pan*. Sexual size dimorphism observed in modern humans is intermediate between that of *Gorilla* and *Pongo* on the one hand, and *Pan* on the other.

Analysis 2 (addressing questions of hypothesis 2.1) assessed sexual dimorphism in vertebral shape at each comparison level and within each taxon: Procrustes distances were calculated between sexes' mean shapes at each comparison level. Significance levels of Procrustes distances between the sexes mean shapes of each taxon were estimated with permutation tests. Results from analysis 2 indicate that modern humans show the most sexual dimorphism in vertebral shape, followed by *Gorilla*. These show significant levels of sexual dimorphism in vertebral shape at comparison levels 1 to 3 (L1 to L3) but not at comparison level 4 (L4). The situation in *Pongo* is ambiguous since results from analysis 2 show large Procrustes distances between *Pongo* male and female mean shapes, indicating large amounts of sexual dimorphism in vertebral shape. However, permutation tests estimate the Procrustes distances not to be significant. This is highly likely due to the small sample size of *Pongo*. Based on the large amount of sexual dimorphism observed in vertebral size in *Pongo* (results of analysis 1), significant amounts of sexual dimorphism in vertebral shape in *Pongo* should have been expected. No sexual dimorphism in vertebral shape was observed in *Pan* (see table 3, permutation tests). In addition, a step-wise discriminant analysis (employing Mahalanobis distances) failed to identify PCs which successfully discriminate between the sexes.

Results from analysis 1 and 2 show that the relative magnitudes of sexual dimorphisms in vertebral size and shape differ considerably between humans, the large sized apes (*Pongo* and *Gorilla*), and the small ape *Pan*. Humans are characterized by more marked differences in vertebral shape than size between the sexes. In the large sized ape *Gorilla* (and presumably *Pongo*), vertebral size dimorphism is more marked than vertebral shape dimorphism. The small ape *Pan* shows the smallest amount of sexual dimorphism in vertebral size and no significant sexual dimorphism in vertebral shape.

Further, results from analyses 1 and 2 confirm the presence of significant differences in vertebral size and shape between the sexes within some of the hominoid taxa in the study. In the following sections, the results from the investigation of the relationships between sexual dimorphism in vertebral size and shape and differences in body weight and locomotion are discussed.

3.6.2 Does sexual dimorphism in vertebral size and shape relate to sexual dimorphism in body weight?

Hypotheses 2.1 (vertebral size) and 2.2 (vertebral shape) were tested to investigate if sexual dimorphism in vertebral size and shape are related to sexual dimorphism in body weight,

To address hypothesis 2.1 (vertebral size), sexual dimorphism in body weight (expressed as ♂/♀ weight ratio) was compared with that in vertebral centroid size (see table 3.5). This comparison shows that a potentially strong relationship between sexual dimorphism in body weight and vertebral size exists within the taxa. To address hypothesis 2.2 (vertebral shape), the same comparison as for hypothesis 2.1 (size) was conducted comparing sexual dimorphism in body weight with that in vertebral shape (see table 3.7). Vertebral shape was represented by Procrustes distances between male and female mean shapes. Results from this comparison show that a relationship between sexual dimorphism in body weight and vertebral shape is weak within the taxa. In conclusion, sexual dimorphism in body weight is associated with differences in vertebral size between the sexes of each taxon. The relationship between sexual dimorphism in body weight and vertebral shape is less obvious.

The second factor this study considered as having a possible association with vertebral size and shape differences between sexes is dimorphism in locomotor repertoires. In the following section the relationships between sexual dimorphism in vertebral size and shape and in locomotor repertoires are discussed.

3.6.3 Does sexual dimorphism in vertebral size and shape relate to sexual dimorphism in locomotor repertoire?

Hypotheses 3.1 (vertebral size) and 3.2 (vertebral shape) were tested to investigate if and how sexual dimorphism in vertebral size and shape is related to sexual dimorphism in locomotor repertoires, - humans have only two modes of locomotion with frequencies about the same between sexes. Apes have more variation in modes and frequencies, humans show mainly differences in walking kinematics due to obstetric functions expressed in variation in pelvic morphology. In great apes, the influences on locomotor kinematics include weight and social factors (resources).

It is not possible to falsify these hypotheses statistically but there does appear to be a relationship between dimorphism of body size and dimorphism of locomotion in that chimpanzees are the least dimorphic on both counts while *Pongo* and *Gorilla* are more dimorphic whereas humans are intermediate. Thus, hypothesis 3.1 is likely falsified. However the finding that humans have a greater degree of lumbar vertebral shape dimorphism (table 3.6) than *Gorilla* is in contrast to the findings with respect to size. This probably reflects a high degree of dimorphism in the mode of locomotion in humans and so is not inconsistent with falsification of hypothesis 3.2, but with respect to the kinematics of modes of locomotion rather than the frequency of use of modes within the locomotor repertoire. As for sexual dimorphism in pelvic morphology in humans and its relationship with locomotor differences see later in the discussion.

In summary, sexual dimorphism in vertebral size is related to differences in body weight, which in turn contribute to differences in substrate usage and hence differences in locomotor repertoires in apes. Sexual dimorphism in vertebral shape on the other hand, is related to differences in the ways in which the sexes move – in part due to body weight (apes) but in part due to other factors such as obstetric functions (humans) and hence differences in locomotion induced by pelvic morphology. In humans in particular, differences in shape between the sexes are expressed as differences in the proportions and relative positions and angulations of vertebral components (e.g. pedicles, vertebral arch etc). These relate directly to the ways in which vertebral processes and vertebral bodies are loaded, indicating mechanical advantages. Therefore, differences in biomechanics of motion are more important in shaping the form of a vertebra than the scaling of loading. This is in contrast to the observations in vertebral size.

The preceding studies have focussed on single lumbar vertebrae. In the following paragraphs sexual dimorphism in patterns of vertebral size and shape variation along the lumbar spine is explored.

3.6.4 To what extent do patterns of inter-segmental shape variation along the lumbar spine differ between the sexes of each hominoid taxon in the study?

With regard to interpreting the fossil record it would be useful if one could draw upon the ways that vertebrae vary in size and shape along the column (metameric variation) as well as the form of individual vertebrae, for instance it may be that differences

between sexes or species are expressed in one or both of these. Thus this part of the study examines the extent to which differences in patterns of metameric variation in size and shape are encountered between the sexes within the various hominoids included in this study.

Thus, hypothesis 4, that there are no differences in patterns of lumbar inter-segmental size and shape variation between the sexes within each taxon in the study was formulated. To test hypothesis 4, the patterns of size and shape variation along the lumbar spine of female and male adult specimens of each taxon are visualized and compared. Results from this analysis show that patterns of vertebral size variation are very similar between the sexes of all taxa. Therefore, there is no sexual dimorphism in patterns of vertebral size variation along the lumbar spine present. The results also show that patterns of vertebral shape variation are virtually the same for both sexes of the great ape taxa. *Homo sapiens* is very different from all great ape taxa in that there is sexual dimorphism observed in the pattern of vertebral shape variation along the lumbar spine. The pattern is most different at the level of L5, indicating that the last lumbar vertebra is very different in shape between the sexes.

Thus since sexual dimorphism is only present in the pattern of human lumbar vertebral metameric shape variation, hypotheses 5.1 (relationship between dimorphism in pattern and centroid size and body weight) and 5.2 (relationship between dimorphism in pattern and locomotion) are tested only for modern humans. With regard to hypothesis 5.1 the results from analysis 5 (differences in patterns) when compared to those from analysis 1 (differences in vertebral centroid size) indicate that there are indeed significant differences in vertebral centroid size between the human sexes, that these correspond with the differences in patterns of metameric variation of vertebral shape. However in the large apes, even larger differences in size are noted between the sexes. Furthermore, male and female humans follow parallel trajectories in the plot of centroid size versus vertebral levels (figure 3.21. This contrasts with the divergent trajectories of shape metamerism in figure 3.22, indicating that size and shape dimorphisms are dissociated. Thus whilst the hypothesis is not falsified in humans it would be unsafe to conclude that dimorphism in patterns of metameric variation of lumbar vertebrae arises as a consequence of size dimorphism. It appears that the pattern of metameric variation in shape in each sex is under the control of influences that are distinct from those regulating the pattern of metameric control of size. With regard to body weight

dimorphism, similar conclusions should be drawn since large apes show even greater weight dimorphism in the absence of dimorphism in metameric patterns of shape variation. Thus, although a body weight difference is found between human males and females, this is unlikely the cause underlying the observed differences in lumbar metameric variation between sexes.

Hypothesis 5.2, (dimorphism of inter-segmental shape variation along the lumbar spine versus dimorphism in locomotion) is tested by comparing results from analysis 5 with the known differences in locomotion between the sexes. Clearly for humans the locomotor repertoire is identical for males and females yet there are known kinematics and kinetic differences between male and female bipedal gaits. Therefore to this degree hypothesis 5.2 is falsified. The differences between male and female bipedalism arises in the main because of obstetric considerations and it may well be that these have the impact on the metameric variation of the shapes of lumbar vertebrae in females noted here. This is discussed in more detail later in this chapter.

Finally preliminary studies examined how sexual dimorphisms in vertebral size and shape arise during the postnatal growth period.

3.6.5 How is sexual dimorphism in vertebral size and shape established during the postnatal growth period?

Dimorphisms in adult lumbar vertebral size and shape likely develop during the postnatal growth period and are possibly established prenatally. Their ontogeny is the focus of the following analyses. To assess how sexual dimorphism in vertebral size and shape is established within the taxa in this study, samples containing (sometimes rather small samples of) infant, juvenile, subadult, and adult specimens of both sexes were explored with GPA/PCA for each taxon. Vertebral size and shape variation between the sexes were visualized by scatter plots of PC1 versus centroid size.

Results from these inevitably preliminary analyses, given poor subadult samples of humans and *Pongo*, indicate that adult males likely extend common size and shape trajectories to larger sizes (shape and size hypermorphosis) at least in *Gorilla*, humans and *Pongo*, albeit that in humans it is possible (but extremely difficult to assess, given the poor subadult sample) that there is some divergence of ontogenetic shape

trajectories between the sexes before adulthood. This will be worth investigating in future studies.

3.6.6 The relationship between sexual dimorphism in body weight, locomotor functions and vertebral size and shape

As seen in the previous paragraphs, sexual dimorphism in vertebral size occurs in all hominoid taxa in this study, whereas sexual dimorphism in vertebral shape is observed only in *Homo sapiens*, *Gorilla* (and potentially in *Pongo*). Metameric patterns of vertebral size variation are not different between the sexes whereas metameric patterns of vertebral shape variation are only different in *Homo sapiens*. Results from testing of hypothesis 2.1 and 2.2 indicate a strong and significant relationship between differences in body weight and vertebral size within each taxon. Body weight dimorphism has a limited relationship with vertebral size too in *Homo sapiens* and *Gorilla*. In *Gorilla*, *Pongo*, and *Homo sapiens*, sexual dimorphisms in vertebral shape between the sexes are principally located in the vertebral body and the vertebral processes but not in the shape and relative diameter of the vertebral canal, nor the articular facets or the superior articular processes.

The impact of sexual dimorphism in locomotion on vertebral size and shape is very difficult to estimate within the framework of this study. However, in the following paragraphs, potential relationships between sexual dimorphism observed in vertebral size and shape within the taxa and sexual dimorphism in body weight and locomotor repertoires will be explored further.

Gorilla gorilla

Differences in vertebral shape in *Gorilla* are highly likely linked to weight bearing functions. This is highlighted by the sexually dimorphic vertebral elements which have been identified previously as the chief weight bearing elements (namely vertebral bodies, pedicles, vertebral arches, and articular processes) of the vertebral column (Adams and Hutton, 1983; Pal and Routal, 1987; Shapiro, 1993a; Slijper, 1946; VanSchaik, 1985). Thus, the anterior wedge shape of the male vertebral bodies is likely a consequence of sexually dimorphism in weight transmission through the lumbar spine.

That great apes and humans have relatively wider and shorter pedicles than other primate species has already been noted by Shapiro (1993a). In this respect, humans are only different from great apes in that their pedicles tend not only to be relatively shorter but also much broader, especially at the level of L5. However, Shapiro (1993a) also noted the lack of a consistent correlation between pedicle shape and body weight. This observation contrasts with the results presented here for *Gorilla* as well as *Homo sapiens*. In the present study, data suggest that male gorillas and humans have relatively broader and shorter pedicles than females. In both, *Gorilla* and *Homo sapiens* forces are not transmitted exclusively through the anterior column as represented by the vertebral bodies but also between the vertebral bodies (first column) and the vertebral arches (posterior column), and thus pass from one to the other through the pedicles (medium column) (Davis, 1961; Pal and Routal, 1987; Shapiro, 1993a). This is because in all hominoid taxa, the vertebral column lies very centrally in the trunk (Schultz, 1933; Schultz, 1961) and because all hominoid taxa show higher frequencies (in the case of *Homo sapiens* exclusively so) of orthograde trunk posture than non-hominoid primates both, during resting and locomotion (Keith, 1903; Schultz, 1933; Slijper, 1946). Due to the larger body weight of humans and *Gorilla* (compared to *Pan*), the pedicles tend to be relatively shorter and stouter to reduce shear stress (Davis, 1961; Shapiro, 1993a). The relatively narrower male vertebral canal probably is the result of the relatively larger vertebral bodies as well as its connection to the relatively shorter and broader male pedicles.

In relation to weight transmission through the vertebral column, one also has to consider that in great apes the flexibility of their lumbar spine is considerably reduced in comparison to either modern humans or non-hominoid primates. This functional region of the vertebral column is shortened and immobilized first through a reduction of the average numbers of lumbar vertebrae, and second, through the decrease in vertebral body length (Schultz, 1938; Schultz, 1961). Further, in great apes, the lumbar spine is usually embedded so deeply between the greatly postero-cranially elongated iliac blades and the last pair of ribs that only L1, L2, and L3 (see figure 3.33) can be flexed and extended to some degree (Schultz, 1969a).

This close proximity of pelvis and rib cage provides an alternative "route" for weight transmission through the trunk, in that weight can directly be transmitted to the pelvis through the rib cage. Also, weight transmission occurs from the lumbar spine to the

pelvis through the iliolumbar ligaments (Hartford et al., 2000; Kapandji, 1992; Slijper, 1946). Thus the proportion of weight transmitted exclusively through the lumbar spine (vertebral bodies, pedicles, articular processes, and vertebral arches) is reduced in great apes when compared to humans. The alternative route of weight transmission via rib cage and pelvis and iliolumbar ligaments to pelvis might explain why the last lumbar vertebra in *Gorilla* is less sexually dimorphic in size (see table 3.1.) than other lumbars and not significantly sexually dimorphic in shape. Therefore, in *Gorilla*, the last lumbar vertebra should be seen as a part of the pelvis rather than a part of the mobile lumbar spine. The alternative weight transmission route is also a good explanation for the finding that the first lumbar element seems to be the most different in shape between the sexes, because it is probably the most mobile vertebra and therefore has to resist the greatest torsion and shear stresses (Schultz, 1969a).

In general, the differences in vertebral shape seen in *Gorilla* lumbar vertebrae are well explained by differences in body weight between the sexes. In *Gorilla*, although there are significant differences in the locomotor repertoire of arboreal and terrestrial locomotion between the sexes (Doran, 1997; Isler, 2005; Remis, 1995), the differences in kinematics of these locomotor modes (at least the climbing ones) are present but smaller than the differences in frequencies of locomotor modes.

The pelvis of *Gorilla* is much less different in shape between the sexes than in humans, and it is almost impossible to estimate the sex of a pelvis except in large adult males where the size makes sex determination clear (Schultz, 1949). Since there are no differences in the pelvic shape of *Gorilla*, and since the lumbar spine seems not to play the same role in generating and maintaining kinetic energy in locomotion as seen in humans (see Chapter I, introduction) no different adaptation in the lumbar spine to locomotor function is necessary between the sexes. However, the large sexual dimorphism in body weight between males and females requires adaptations to resist the substantial forces transmitted through the lumbar spine. Thus, although the locomotor repertoire is different between the sexes, locomotor kinematics are less so and this is also expressed in the postcranium showing no difference in the areas (pelvis, lumbar spine) which are crucial for locomotor biomechanics of modern humans.

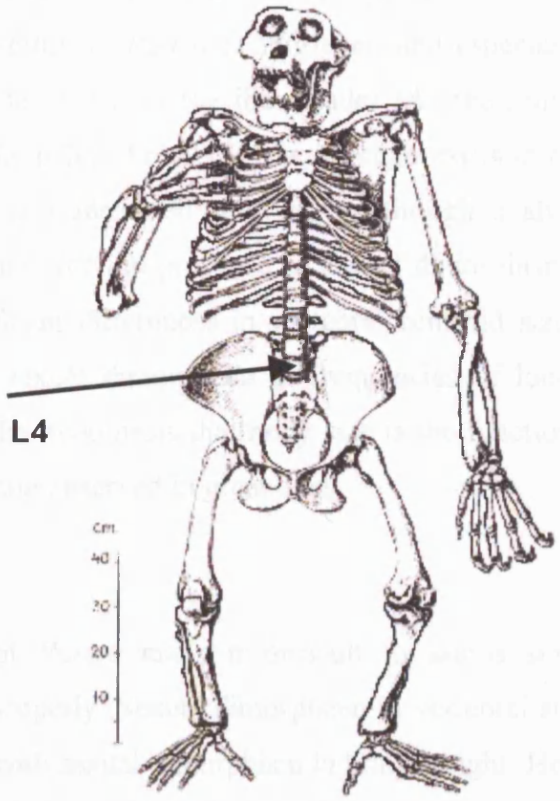


Figure 3.33 Male *Gorilla* skeleton: last lumbar vertebra is deeply wedged between the iliac blades. From Schultz (1969a), p.77

Sexual dimorphism in vertebral size and shape in *Gorilla* could therefore be considered as the result of ontogenetic scaling. Other workers exploring the ontogeny of sexual dimorphism in the *Gorilla* postcranium reach similar conclusions. For example, Taylor (1997a) demonstrates that *Gorilla* males and females are ontogenetically scaled for postcranial body proportions. The same is to be said for scapular dimensions (Taylor, 1995; Taylor, 1997). Results from the present study seem to corroborate these results: the trajectories of ontogenetic vertebral size and shape variation share the same slope but the male trajectory is elongated compared to the female one.

Pan troglodytes

In the case of chimpanzees, no differences in vertebral shape were found between the sexes. However, significant differences in the preference of substrate (arboreal, terrestrial) are observed (Doran, 1993a; Doran, 1993b; Remis, 1995) between the sexes in *Pan*. Therefore, differences in frequencies of locomotor modes are observed, as summarized earlier in this chapter. However, kinematics between males and females in *Pan* are clearly less impressive than those observed within *Gorilla* and *Pongo* (Isler,

2005; Isler and Thorpe, 2003). The same can be said for the limited mobility of the lumbar spine (Schultz, 1969a): in *Pan* it is shortened and especially the last presacral vertebra is deeply embedded between the iliac blades. As the same alternative weight transmission route from the pelvis directly to the rib cage exists in *Pan* as in *Gorilla*, at least part of the weight is transmitted this way. Although analysis 2 did not yield statistically significant results for the presence of sexual dimorphism in vertebral shape, there are small but significant differences in vertebral centroid size observed between the sexes. Thus, despite sexual dimorphism in frequencies of locomotor modes, this lends further support to the hypothesis that body size is the functional denominator for differences in vertebral shape observed in great apes.

Pongo pygmaeus

The small sample size of *Pongo* made it difficult to assess sexual dimorphism in vertebral size and shape properly. Sexual dimorphism in vertebral size is clearly present and has a strong relation with sexual dimorphism in body weight. However, results from the investigation of sexual dimorphism in vertebral shape are ambiguous: values for differences in vertebral shape between the sexes are high, yet statistical tests did not yield confirmation of statistical significance of these results. Given the large sexual dimorphism in body weight and vertebral size and the similarity of size and shape variation patterns with other great apes, it is probably safe to assume that significant sexual dimorphism in vertebral shape occurs in *Pongo* but the sample used in this study is inadequate to confirm this. Trajectories of intra-specific vertebral size and shape variation between various age groups are likely similar to those of *Gorilla*. Patterns of vertebral size and shape variation along the lumbar spine are not different between the sexes in *Pongo* when compared to other great ape taxa.

Based on these findings, it is assumed that sexual dimorphism in vertebral size and shape in *Pongo* varies in relation to body weight and weight transmission dimorphism. In this, *Pongo* presumably resembles *Gorilla* (the other large ape with considerably dimorphic body weight); hence males and females are ontogenetically scaled in relation to each other and in relation to vertebral shape. To statistically support these interpretations however, a more extensive study of a larger sample (containing both adult and immature specimens of both sexes) of *Pongo* specimens would be necessary.

Homo sapiens

Regarding intra-specific differences in vertebral size and shape between the sexes of *Homo sapiens* indicate that these are highly significant at all vertebral comparison levels. The magnitude of differences in size between the sexes is greater in *Homo sapiens* than in *Pan* but smaller than those observed in *Gorilla* and *Pongo*. Interestingly, the vertebral shape differences recorded for *Homo sapiens* are greater in magnitude than those observed in *Gorilla.* Consequently, *Homo sapiens* displays the greatest degree of sexual dimorphism in vertebral shape.

Sexual dimorphism in human vertebral size and some aspects of sexual dimorphic vertebral shape are highly likely related to sexual dimorphism in body weight. In humans, weight transmission occurs entirely through the upright vertebral column. In upright trunk posture, the weight supporting area (vertebral bodies) is small therefore the smaller human body weight dimorphism (compared to e.g. *Gorilla*) can still have a strong impact on vertebral size and also on vertebral shape between the sexes. Thus, shape differences such as the relatively broader, wider and - most importantly - shorter male lumbar vertebral bodies, in combination with relatively shorter and broader male pedicles should be viewed in regard to sexual dimorphism in body weight.

Adaptations such as the pronounced posterior wedge shape of vertebral bodies and broader vertebral arches in female *Homo sapiens* on the other hand, might be related to sexual shape dimorphism seen in the human pelvis and sacrum. This assumption might be corroborated by the results from the analysis of the shape variation patterns (analysis 5): they do not vary much between the sexes at comparison levels 1 to 4. At comparison level 5, on the other hand, shape dimorphism is substantial. If pelvic and sacral dimorphism somehow is related to sexual dimorphism in vertebral shape, the last presacral vertebra would be expected to be the most dimorphic in shape on the grounds of proximity and its functional consequences.

In humans, the pelvis is markedly dimorphic. The shape differences are significant enough to serve as reliable traits for sexing skeletal material of previously unknown sex, a technique that is often used in forensic and archaeological studies (Genovés, 1959). The sexual shape dimorphism observed in the sacrum too should be considered in this context. The sacrum is an integral a part of the pelvis. Its shape is therefore contributing to the overall shape of the pelvic girdle. Sexual shape dimorphism of the sacrum is less

obvious than that of the pelvis, but a trained researcher is able to reliably estimate the sex of an individual based on its sacrum. This is because males have longer *Alae* relative to the medio-lateral diameter of the superior body surface of the first sacral vertebra. In females, the width of the body surface equals the length of the *Alae* (Anderson, 1962).

Shape differences in the pelvis and sacrum are explained partially as adaptations to obstetric functions which, to a certain degree, coincide with adaptations of the human pelvis to habitual bipedal gait. For example, the distance between the sacroiliac joints and the hip joint is considered to be highly influential on both, the size of the birth canal as well as the extent of leverage of the hip adductor muscles (Steudel, 1981). Also, as noted by Tague (1992), the dimensions of the pelvis that are most dimorphic in relation to obstetric functions, are the measures of the posterior space, the bi-ischial breadth, the sub-pubic angle, and the angulation of the sacrum and these are larger in females than males. The larger female angulation of the sacrum requires compensation in the form a larger lumbar lordosis to maintain the trunk permanently over the pelvis. That women do indeed have a larger lumbar lordosis has been noted by different authors (Cheng et al., 1998; Fernand and Fox, 1985). The more pronounced posterior wedge shape of female lumbar vertebral bodies can therefore be interpreted as a consequence of the larger degree of lumbar lordosis. The greater opening of the *Incisura vertebralis major* of female humans has been described as trait that is also directly linked to enhancing the lumbar lordosis (Martelli and Schmid, 2003).

The analysis of human ontogenetic vertebral shape variation between the sexes was not informative but it would be of interest in future studies to compare the trajectories of ontogenetic shape variation of the pelvis and sacrum between the sexes. Previous studies indicate differences between the sexes in human foetal pelvic shape (Holcomb and Konigsberg, 1995). However, the differences in shape were too small to serve as a reliable sex determinant of skeletal remains.

One could argue that vertebral shape differences in the lumbar spine are the expression of adaptations which guarantee the same degree of energetic efficiency of bipedal gait in both sexes. As previously mentioned in Chapter I, (pp. 44 onward), the lumbar spine is a key element in maintaining and storing kinetic energy in locomotion. Although kinematics of human bipedal gait differ between male and female humans, in general,

the lumbar spine performs the same role during locomotion in both sexes. The larger female lumbar lordosis (Cheng et al., 1998; Fernand and Fox, 1985) could be seen in relation to the increased female angular rotation of the lumbo-pelvic–hip complex during walking (Schache et al., 2003). The more pronounced posterior wedge shape of the female vertebral bodies and more posterior angulation of the vertebral arches could be interpreted as mechanical consequences of the more accentuated female lumbar lordosis in relation to bipedalism.

3.6.7 Summary

In this chapter, the intra-specific shape and size differences of single lumbar vertebrae of *Gorilla gorilla*, *Pan troglodytes Pongo pygmaeus* and *Homo sapiens* have been investigated. Additionally, the pattern of shape and size differences along the lumbar spine of each species has been described and discussed.

Gorilla gorilla expresses a high degree of body size dimorphism and has lumbar vertebrae which are sexually dimorphic in size. They also are sexually dimorphic in shape with the exception of the last presacral vertebra. Sexual dimorphism in vertebral shape is related to sexual dimorphism in body weight. Patterns of size and shape variation along the lumbar spine are not sexually dimorphic. Sexual dimorphism seems to develop through an extension of ontogenetic trajectories in size and shape in males.

Pan troglodytes displayed a small amount of sexual size dimorphism but no sexual dimorphism was registered in vertebral shape. This is interpreted as a consequence of the smaller sexual dimorphism in body weight. Patterns of size and shape variation along the lumbar spine are not sexually dimorphic. Trajectories reflecting vertebral size and shape variations between age groups (infants to adults) are similar for males and females.

Pongo pygmaeus expresses a high degree of body size dimorphism, and has lumbar vertebrae which are sexually dimorphic in size. They also are sexually dimorphic in shape with the exception of the last presacral vertebra. Sexual dimorphism in vertebral shape is related to sexual dimorphism in body weight. Patterns of size and shape variation along the lumbar spine are not sexually dimorphic. From a very limited

sample sexual dimorphism seems to develop through extension of ontogenetic trajectories in size and shape in males as in *Gorilla*

Homo sapiens shows body weight dimorphism which smaller than that observed in the modern great ape taxa. Vertebral size and shape are significantly different between the sexes. Some of the shape differences can be attributed to the unique human weight transmission mechanism in relation to upright posture and body weight dimorphism. However, some of the shape differences seem to be linked to functions of the lumbar spine in locomotion (degree of lordosis) and the fact that humans have extremely sexually dimorphic pelves and sacra. The adaptations of the lumbar spine seem to compensate for the differences in shape of the pelvis to guarantee energetic efficiency of male and female bipedalism. Patterns of vertebral size variation are not sexually dimorphic, but patterns of shape variation are for the last lumbar. These results corroborate the assumption that sexual dimorphism in vertebral shape is related to sexual dimorphism in pelvic and sacral morphology. Human postnatal ontogeny of vertebral size and shape differs from all great apes. The subadult sample of humans is inadequate to assess if sexual shape dimorphism is established purely through extension of shared ontogenetic size and shape trajectories in males relative to females or whether these diverge.

3.7 Conclusions

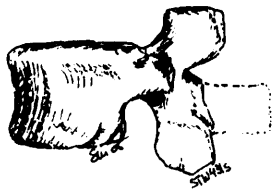
In summary, results from the present study indicate that differences in body weight in highly sexually size dimorphic hominoids (*Gorilla, Pongo*) impact on vertebral size and shape. In small bodied apes (*Pan*), vertebral size is related to differences in body weight, but no sexual dimorphism is seen in vertebral shape. We can therefore conclude that in the living great ape taxa, body weight dimorphism impacts on vertebral shape, whereas sexual dimorphism in frequencies of locomotor repertoires and locomotor kinematics do not show a relation to vertebral shape.

Modern humans differ from great apes. Differences in vertebral shape not only correlate with body weight but also with sexual dimorphism in pelvic and sacral morphology. Thus, sexual dimorphism in vertebral shape not only is related to body weight dimorphism but also to obstetric functions. The fact that a the smallest observed ♂/♀ weight ratio is paired with sexual dimorphism in vertebral size larger than that of *Pan*

could be related to the absolute larger body weight of *Homo sapiens* (compared to *Pan*) as well as to the habitual upright trunk posture of humans (see chapter IV for further discussion of this point).

3.7.1 Implications of the investigation of sexual dimorphism in fossil hominoid lumbar vertebral size and shape

For the future study of fossil hominid (australopithecine) lumbar vertebral material, these findings have important consequences. Sexual dimorphism in locomotor repertoires, which consist of differences in frequencies of locomotor modes, are highly likely not related to sexual dimorphism in lumbar vertebral size and shape.



CHAPTER IV, INTER-SPECIFIC VERTEBRAL SIZE AND SHAPE VARIATION

The lumbar spine of *Gorilla gorilla, Pan troglodytes, Pongo pygmaeus,* and *Homo sapiens* reflects differences in locomotor functions rather than phylogenetic background or inter-specific differences in body weight

4.1 Introduction

This study examines the inter-specific variation in lumbar vertebral morphology in several hominoid taxa and considers the extent to which this variation is influenced by inter-specific differences in locomotor repertoires, body weight, weight transmission mechanisms, and phylogenetic history. Further, differences in the postnatal ontogeny of inter-segmental shape variation patterns along the lumbar spine are explored to establish how the inter-specific variation, observed in the adult lumbar spine, developes (shape change vs. time) postnatally.

Molecular data suggest that humans and chimpanzees are more closely related to each other than either is to gorillas. Yet the similarity of chimpanzee and gorilla morphology and locomotor behaviour is far greater than between any of the great apes and modern humans. Patterns of clustering based on phylogeny (based on molecular biology) will be compared to patterns of clustering based on vertebral shape. Hypotheses will be tested that are falsified if clustering patterns based on phylogeny and vertebral shapes are not congruent. In that case, an attempt will be made to relate inter-specific differences in lumbar spine anatomy with factors of interest, namely locomotion and weight bearing. In this context, the extent to which postnatal ontogenetic lumbar shape trajectories reflect clustering patterns based on phylogeny and vertebral will also be investigated.

The major goal of this study however, is to provide a comparative framework, within which fossil hominoid lumbar vertebral material can be compared to humans and apes and related to the differences between extant taxa and their phylogenetic and functional correlates.

4.2 Background

Locomotor affinities of fossil hominins are subject to ongoing debates. Whereas more "recent" hominid taxa, such as *Homo erectus* (Ruff and Walker, 1993) or *Homo neanderthalensis* (Shackelford and Trinkaus, 2002; Stringer and Gamble, 1993; Trinkaus and Ruff, 1999a; Trinkaus and Ruff, 1999b) are widely thought to be exclusively bipedal in the same manner as modern humans, opinions vary for earlier hominin taxa such as *Homo habilis* (Häusler and McHenry, 2004; Susman and Stern, 1982) or the australopithecines (Häusler, 1992; Stern and Susman, 1983; Stern et al., 1984). The biomechanics and frequencies of bipedalism were probably highly diverse in the early hominin taxa (Harcourt-Smith and Aiello, 2004). Thus, the current opinion holds that australopithecines walked bipedally when on the ground and that bipedalism played an important enough role in their locomotor repertoire so as to be associated with substantial anatomical changes promoting its efficiency. It is widely held that the australopithecine manner of bipedalism was recognizably different from that practised in modern humans (Berge, 1994; Crompton et al., 1998; Kramer, 1999; Rak, 1991; Stern and Susman, 1983; Ward, 2002; White and Suwa, 1987; Zihlman and Hunter, 1972; Zuckerman et al., 1973). On the other hand, adaptations to arboreal locomotion are clearly present in their postcranial morphology (Inouye and Shea, 1997; Latimer, 1991; Pontzer and Wrangham, 2004; Schmid, 1983; Sellers et al., 2003; Sellers et al., 2004; Stern et al., 1984; Ward, 2002; Zuckerman et al., 1973). However, to what degree their arboreal locomotion resembles that of African or Asian apes - if at all - is not clear. Several studies have examined the morphology of the lumbar spine of fossil hominins, namely *A. africanus* and *A. afarensis*, in order to address this question. Both *A. africanus* and *A. afarensis* possess aspects of lumbar morphology different from both modern humans and modern great ape taxa (Benade, 1990; Martelli and Schmid, 2003; Robinson, 1972; Sanders, 1998; Shapiro, 1993a). These differences in specific features imply that the locomotion of australopithecines was both different from that of modern great apes and modern *Homo sapiens.*

To what degree the overall shape of their lumbar vertebrae really differs from different great ape taxa as well as from modern humans is not completely resolved. It is not known how much of the differences in size and shape observed between humans and australopithecines and great apes and australopithecines is attributable to specific adaptations to locomotion, body weight, and most importantly: phylogenetic history. After all, the similarity in vertebral shape of modern humans and australopithecines

might reflect the close phylogenetic relationship between them rather than differences in bipedal biomechanics. Therefore, it is important to understand the differences in lumbar size and shape between the modern hominoid taxa and to be able to interpret them in relation to differences in locomotion, weight transmission, body weight, and phylogenetic history.

The lumbar spine was chosen for investigation because the morphological variations observed in land living mammals broadly reflect differences in locomotor repertoires and positional behaviour (Boszczyk et al., 2001; Gal, 1993; Slijper, 1946). The lumbar spines of both, fossil and modern primates are no exception, as has already been shown elsewhere (Badoux, 1974; Johnson and Shapiro, 1998; Martelli and Schmid, 2003; Robinson, 1972; Sanders, 1998; Schultz, 1961; Slijper, 1946). That the lumbar spine of primates with highly specialized locomotor repertoires such as the vertical climbing and leaping indrids or the habitually bipedal humans show adaptations to their respective locomotor behaviour comes therefore as no surprise (Schultz, 1950a; Schultz, 1961; Schultz and Straus, 1945; Shapiro, 1995). On the other hand, it is less clear, how differences between the locomotor repertoires of modern great apes relate the morphology of their lumbar spines.

4.2.1 The locomotor repertoires of modern hominoids

All primates (including hominoids), although fundamentally quadrupedal in design, like the majority of other mammals, show (with the exception of humans) considerable flexibility in their locomotion; they combine arboreal and terrestrial locomotor modes in their locomotor repertoires (Schultz, 1969a).

The terms "locomotor repertoire" and "locomotor modes" are often used in describing and discussing the locomotion of primates e.g. (Doran, 1992; Doran, 1993a; Hunt et al., 1996; Inouye and Shea, 1997; Jablonski, 1993; Sellers, 1996). These terms are sometimes used interchangeably or it is not entirely clear what they cover. In this study, "locomotion" is used as a general term that describes

"*the ability of self-powered, patterned motion of limbs or other anatomical parts by which an individual customarily moves itself from place to place" (Wikipedia, 2005)*

"Locomotor mode" is used as a substitute for locomotor activity. It describes a particular type of locomotion; in primates this can be e.g. climbing, walking, leaping, running or others. The term "locomotor repertoire" on the other hand, describes the entire range of locomotor modes, which is used by a particular primate taxon. Thus, during locomotion, different hominoids manifest different locomotor repertoires. These may vary both in their constituent locomotor modes and the frequencies of use of these modes.

Between different hominoid taxa, any given locomotor mode may show subtle differences. For example, the kinematics of vertical climbing of African apes differ from those of Asian great apes (Isler, 2005). Also, the biomechanics of modern human bipedal gait differ from that of great apes (Jenkins, 1972; Tardieu et al., 1993). In the following paragraphs, short summaries of the locomotor repertoires of all taxa in this study are presented.

Modern humans

The diversity of the locomotor repertoire of modern humans –compared to other hominoids – is relatively limited. It consists exclusively of bipedal walking and running. First attempts at bipedal walking start around the age of 10 to 18 months, and become more adult-like in terms of stride frequency, phase swinging, and heel-strike, between the age of 50 to 90 months (4 to 7 years) (Vaughan et al., 2003). Before the age of 10 months, humans engage in other forms of "locomotion", of which crawling is the most frequent.

African apes

The African ape locomotor repertoire is far more diverse than that of humans. In trees, African apes preferably hang under the substrate rather than walk quadrupedally on it – hence their classification as suspensory climbers (Fleagle, 1992; Hunt, 1991b; Keith, 1903; Schultz, 1969a). African ape terrestrial quadrupedal locomotion consists predominantly of knuckle-walking (Tuttle and Basmajian, 1974). Besides knuckle-walking, short periods of bipedalism have been reported for both *Gorilla* and *Pan* (Doran, 1993b; Doran, 1997; Remis, 1995).

Asian apes

In contrast to African great apes, *Pongo* is a predominantly arboreal primate and does not travel on the ground very often (Hunt, 1991b; Sonntag, 1924). They are also the largest living canopy-dwelling animals (Delgado and Van Schaik, 2000). The arboreal locomotor repertoire is highly diverse and consists of high frequencies of hand-foot hanging, bipedal postures, clambering, bridging and true brachiation (Cant, 1987a; Hunt, 1991b; MacKinnon, 1974). In the relatively rare periods (compared to African apes) when orang-utans do travel on the ground, they walk on the lateral rims of their fists (clenched to various degrees) (Sonntag, 1924). Hence the term "fist-walker" (Tuttle and Basmajian, 1974) has been coined.

4.2.2 Differences in the locomotor repertoires of extant great apes

The locomotor repertoires of both *Pan* and *Gorilla* differ more from *Pongo* than they differ from each other (Hunt, 1991b). The differences in terrestrial locomotion between Asian and African apes have been summarised above. In arboreal locomotion, orang-utans climb more slowly, with longer strides and in general with more motion in the major limb joints than the African apes (Isler, 2005).

Differences between the African ape taxa seem predominantly to consist of higher flexibility in the climbing performance of the smaller sized apes (e.g. bonobos) in comparison to larger apes (gorillas) (Isler, 2005). Also, despite the similar vertical climbing performances of bonobos and gorillas, the frequencies of arboreal locomotor modes are not similar; *Gorilla gorilla* spends less time in trees than does *Pan troglodytes* (or *Pan paniscus*) (Cant, 1987b; Hunt, 1991b). Once in the trees, *Gorilla gorilla* engages in suspensory climbing less often than *Pan* (Doran, 1997). Differences in the frequencies of use of different locomotor modes are also observed at the sub-species level: e.g. mountain gorillas (*Gorilla gorilla beringei*) seem to spend considerably less time in trees and thus are less engaged in arboreal locomotion than the lowland species (*Gorilla gorilla gorilla*) (Taylor, 1997). Differences in locomotor repertoire consisting of differences of frequencies of use in locomotor mode are also observed between the sexes. (Remis, 1995; Remis, 1999) finds that male gorillas, when compared to females, climb trees less frequently and if they do climb, they stay closer to the core and do not forage too far into the tree periphery. The same is also observed in chimpanzees. Both *Pan paniscus* and *troglodytes* females, spend considerably more

time in the trees than the males. (Isler, 2005) observed that male gorillas are less apt in climbing vertical substrates than females and juveniles. In general, juveniles engage more often in arboreal locomotor behaviour than adults do in both African ape taxa (Doran, 1997).

4.2.3 How do inter-specific differences in locomotor repertoires influence the morphology of the lumbar spine?

Differences in the locomotor repertoire of hominoids are most likely expressed in variation of the orientation and size and shape of the costal processes as well as the spinous process. This is because these structures are in functionally close association with the spinal ligaments and the epaxial back muscles (Boszczyk et al., 2001; Shapiro, 1990; Slijper, 1946). The differences observed in lumbar spine morphology between great apes and modern humans are best explained as adaptations to the permanently upright body posture and habitual bipedalism of the latter. For example, the presence of a permanent lumbar lordosis in the modern human spine, which is largely absent in great apes (Schultz, 1961) is generally interpreted as an adaptation to habitual bipedalism (Gracovetsky, 1985; Robinson, 1972; Sanders, 1998; Schultz and Straus, 1945). The advantage of a permanent lordosis is that this curvature can act as a thrust damper during bipedal gait (walking but especially running). Additionally, the lumbar lordosis is crucial in maintaining the trunk permanently erect over the hip joints.

4.2.4 The influence of overall body weight and weight transmission through the spine on the size and shape of the lumbar vertebrae in hominoids

In the case of great apes and modern humans, there are considerable differences in body weight observed between the taxa. Although there are some difficulties in determining the average body weight of great apes as well as modern humans, the following data were compiled from various sources in the literature (Delgado and Van Schaik, 2000; Jungers, 1985a; MacKinnon, 1974; Nowak, 1999; Plavcan and Van Schaik, 1997; Rowe, 1996; Ruff, 1991). Since the species means for body weights were compiled from various literature sources and since these sources vary to some degree, it was decided to represent the mode for each species. This had the advantage of reducing the influence of outlier data (zoo animals!) on the species mean and give an impression as to where the majority of the literature data was clustered. On average, *Gorilla* is the

heaviest, *Pan* the lightest. Regarding sexual dimorphism, *Gorilla* manifests the highest degree of sexual dimorphism in body, followed by *Pongo*. *Pan* shows a slightly larger weight dimorphism than *Homo sapiens* (see table 4.1).

Sex	*Homo sapiens*	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*
Female	**55** ± 4.62 (1sd = 2.31)	**91.4** ± 23.6 (1sd = 11.8)	**38.1** ± 5.0 (1sd = 2.5)	**38.2** ± 3.0 (1sd = 1.5)
Male	**68** ± 15.5 (1sd = 7.75)	**177.8** ± 47.2 (1sd = 23.6)	**49.2** ± 9.8 (1sd = 4.9)	**75.7** ± 10.0 (1sd = 5.0)
♂/♀ **Weight ratio**	**1.2 120%**	**1.95 195%**	**1.3 130%**	**2.0 200%**

Table 4.1 Male and female hominoid body weights in kg. ♂/♀ weight ratio in %.Values are compiled from the following sources: Delgado and Van Schaik (2000), Jungers (1985a), MacKinnon (1974), McHenry (1992a,b), Nowak (1999), Plavcan and Van Schaik (1997), Rowe (1996), and Ruff (1991)

4.2.5 Differences in overall body weight of hominoid primate taxa- allometry

Basic biomechanical principles predict that inter-specific differences in body weight should impact on the morphology of the axial skeleton. Of greatest interest in this context is weight transmission through the lumbar spine in relation to size and posture. The habitual posture of various taxa is influenced by their locomotion. Naturally, in heavier taxa, more weight is transmitted through the vertebral column. The lumbar spine will adapt to these higher loads in heavier taxa. On the other hand, the proportion of body weight that is transmitted through the vertebrae of the lumbar spine is different if the trunk is held in pronograde or orthograde position. Further the differences in trunk position also influence the ways in which body weight impacts the morphology of lumbar vertebrae. Thus, body weight has a more profound effect on the shape of more caudal vertebrae in the habitually erect trunk of humans than it does on the more cranial vertebrae. Therefore, in interpreting differences in vertebral morphology it should be borne in mind that these might relate to differences in locomotion (e.g. bipedal humans vs. quadrupedal apes), differences in body weight (*Gorilla* vs. *Pan*), or some combination of the two.

In this context, the fact that many anatomical features vary with body size and body weight in a non-linear fashion has to be considered (Jungers, 1978; Jungers, 1985b). Instead, there is a curvilinear relationship between dimensions of functional systems and body weight – called allometry (Martin, 1990). Investigating allometric effects is helpful in identifying fundamental scaling principles and to highlight convergent responses to constraints imposed by body size. In related taxa such as hominoids, differences in body weight are described as "scaling" which can be defined as the structural and functional consequences of differences in size among organisms of more or less similar design (Jungers, 1985b). Thus how body weight variation in hominoids influences behaviour, ecology, anatomy and physiology, as well as evolution is of great interest.

4.2.6 How do inter-specific differences in body weight transmission and posture in relation to locomotion influence the morphology of the lumbar spine?

Adaptations to weight bearing function are expressed as variations in size and shape of the lumbar vertebrae and as variations in the patterns of inter-segmental shape changes of the weight bearing vertebral structures such as the vertebral body, articular processes, and pedicles. As noted earlier, they vary according to differences between taxa in the proportions of body weight transmitted through them and according to locomotor repertoire, and the genetic program (e.g. number of lumbar vertebrae) (O'Higgins and Johnson, 1993; Richardson et al., 1998; Rose, 1975; Schultz, 1931; Schultz, 1961; Shapiro, 1993b). Thus, hominoid lumbar vertebrae are characterized by being more robust and larger than the ones of non-hominoid primates (Rose, 1975; Schultz, 1953; Shapiro, 1993a). Hominoid vertebrae have large vertebral bodies and robust stout pedicles. Modern humans possess the relatively most robust vertebrae and, in their last lumbar vertebra, the most robust pedicles (Rose, 1975; Shapiro, 1993a). Also, the lumbar spine of hominoids is – in comparison to non-hominoid primates – relatively short (Keith, 1903; Schultz, 1938; Schultz and Straus, 1945). The reduction of the lumbar spinal length is achieved by a) a reduction in vertebral body length and by b) a reduction of the lumbar vertebral numbers in relation (Schultz, 1938; Schultz and Straus, 1945). Phylogenetic history of the inter-and intra-specific variation of the number of lumbar vertebrae in the hominoids has been discussed elsewhere (Häusler et al., 2002; Pilbeam, 2004; Sanders, 1994; Schultz, 1938; Schultz and Straus, 1945). The shorter spine and large vertebral bodies reduce the bending stresses caused by the large

body weight of hominoids on single vertebrae and the lumbar spine as a whole (Rose, 1975). However, the shorter lumbar spine also reduces the flexibility of the trunk and thus provides – at least in the great ape taxa - a stable base for the insertion of the musculature relevant for climbing locomotion (Hunt, 1991a).

4.2.7 Phylogenetic history

It is of great interest to see how phylogenetic history influences the overall shape of the lumbar spine because this impacts on comparative studies of modern humans and fossil hominids. Phylogenetic analyses of the hominoid taxa in this study, based on molecular data (Andrews and Martin, 1987; Gagneux et al., 1999; Ruvolo et al., 1991; Ruvolo et al., 1994), presently support the view that *Homo sapiens* and *Pan troglodytes* are sister taxa whose nearest relative is *Gorilla gorilla. Pongo pygmaeus*, on the other hand, is most distantly related to the combined *Homo*/African ape clade. For ease of reading, figure 1.1 from Chapter 1 (introduction) is reproduced as figure 4.1 here.

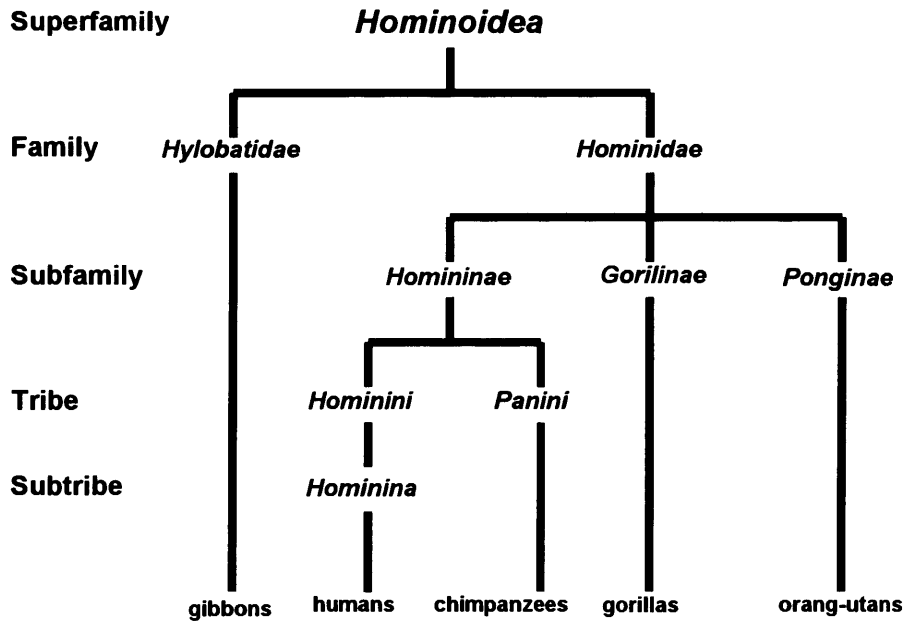


Figure 4.1 Hominoid taxonomy after Wood and Richmond (2000a). It recognizes the close genetic links between *Pan* and *Homo*. "Branch length" is not consistent with phylogenetic distances

Since *Homo sapiens* and *Pan* are the closest living relatives, it can be expected that they share similar spinal anatomies. However, since the locomotor repertoires of *Pan* and *Gorilla* resemble each other more than those of *Pan* and *Homo sapiens*, they probably

share a more similar morphology of the lumbar spine than would be expected based on the molecularly established phylogeny. Thus, it is interesting to investigate how phylogenetic relationships and function (locomotion) influence the shape of the lumbar spine of the four taxa. Any similarities observed in *Pan* and *Gorilla* to the exclusion of *Homo sapiens* might be attributable to function rather than phylogeny. Conversely modern humans are probably closely related to australopithecines, similarities in the morphology of their vertebrae might be attributable to phylogeny rather than function. For these reasons it is important to understand the relative impact of function and phylogeny on the lumbar vertebral morphology in order to provide the proper framework to interpret fossil material.

4.2.8 Ontogenetic allometry and how inter-specific differences in size and shape change towards adult vertebral shape

The extent to which different taxa show parallel or divergent ontogenetic shape trajectories depends to a large degree on the extent to which their ontogenetic changes in morphology are controlled. Vertebral form is to a considerable degree determined through initial patterning and proportioning of skeletal and connective tissues under tight genetic regulation (Burke et al., 1995; Fromental-Ramain and al., 1996; Johnson et al., 1989; Krumlauf, 1994; Peters et al., 1999; Wellik and Capecchi, 2003). Beyond this, pre-and postnatal ontogenetic changes are modulated by local function and spatial cues from adjacent soft tissues and functional spaces. Influences that determine local changes of vertebral features include the genetic program determining the form of cartilaginous elements, the effects of soft tissue growth, hormones, and local biomechanics.

4.3 What is new in the present study?

The study will look at differences in lumbar morphology of great apes and modern humans and relate these to size, locomotion and phylogeny. Inter-specific differences in vertebral size and vertebral features between modern humans and great ape taxa have been documented previously (Rose, 1975; Sanders and Bodenbender, 1994; Schultz, 1933; Schultz and Straus, 1945; Shapiro, 1993a; Shapiro, 1993b). However, this study also aims at novelty here in that we investigate how inter-specific differences in adult hominoid lumbar morphology are established throughout postnatal ontogeny. Are the differences in size and shape already present in the sub-adult specimens, or are they

rather similar with differences in vertebral size and shape between the taxa becoming established later in life? Thus, in studying the postnatal ontogeny of lumbar morphology, we aim to relate ontogenetic allometry to inter-specific differences in size and shape and investigate the extent to which these arise through ontogenetic scaling. The objective is to add new and useful information as to how the ontogeny lumbar spine relates to locomotion, body weight and phylogenetic history. If inter-specific differences in patterns of inter-segmental size and shape variation along the lumbar spine are established early on in ontogeny, this indicates that they are under strong genetic control. However, if these differences are established later in ontogeny, they are likely influenced by function.

Another novelty in this study is the investigations of inter-segmental (metameric) patterns of shape variation. A similar investigation of the spine of mice and humans in two dimensions provides interesting insights into the mosaic nature of vertebral column evolution in that it was shown that certain vertebral features (e.g. vertebral canal dimensions) are highly conservative in their patterns of metameric variation whereas others (e.g. spinous process) are not (O'Higgins, 1997). Those features that are most plastic are those that are most intimately involved in locomotor functions. Since no attempt at an integrated comparison of inter-segmental shape variation of the lumbar spine of hominoids has been carried out so far, it is of great interest to apply such approaches to the investigation – in three dimensions – of the lumbar spine of closely related taxa such as the modern hominoids.

The methods employed in this study to investigate lumbar vertebral morphology are from the field of geometric morphometrics and contrast with the ones used in previous studies. Previously, studies of the hominoid lumbar spine have predominantly relied on traditional approaches to the investigation of variation in morphology. In contrast to geometric morphometric methods these approaches are based on multivariate analyses of collections of inter-landmark distances, ratios and angles (Dryden and Mardia, 1998). These typically only represent part of the information that may be obtained from the position of the landmarks on which the measurements are based. The traditional methods do not take into account information about the spatial relationships among the measured variables (Rohlf, 1999). Intuitively, one expects methods that take the full 3-D information into account to have greater statistical power to detect differences in overall shape or co-variation with other variables (Rohlf, 1999). Another advantage of

geometric morphometric methods is that the multivariate analyses of shape variables allows visualization of the actual shapes corresponding to points in the multivariate space of the analysis (Rohlf, 1999). The geometric morphometric approach provides a well understood statistical framework in which the variation of vertebral size and shape morphology can be investigated. Therefore, this study employs geometric morphometric methods to access the high-dimensional complexity of the overall form of lumbar vertebrae and the lumbar spine as a whole.

4.3.1 The aims of the present study

The specific aims were summarized as follows:

1. To confirm that differences in lumbar vertebral size and shape exist between *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*
2. Once confirmed, to investigate if these differences in vertebral size and shape are related to inter-specific differences in body weight, inter-specific differences in locomotor repertoire and phylogenetic history
3. To assess the extent to which the patterns of inter-segmental shape variation along the lumbar spine differ between the four hominoid taxa in the study and how these differences are established throughout postnatal ontogeny

To these ends the following hypotheses will be tested:

Hypothesis 1

The first hypotheses examine the extent to which there are differences in vertebral size and shape between the taxa.

- **Hypothesis 1.1:** There are no differences in vertebral centroid size between the four hominoid taxa in the study

  This hypothesis will be **falsified** if statistically significant differences in vertebral centroid size are identified for one or more of the taxa in the study.

- **Hypothesis 1.2:** There are no inter-specific differences in vertebral shape observed between the four hominoid taxa in this study

This hypothesis will be **falsified** if statistically significant differences in vertebral shape are identified between the four hominoid taxa in the study.

Hypothesis 2

It there are inter-specific differences in size and shape between the four hominoid taxa (hypothesis 1.1 and 1.2 falsified), the second hypothesis examines the extent to which the differences in vertebral size and shape relate to differences in body weight between the taxa.

- **Hypothesis 2.1:** There is no relationship between patterns of vertebral size variation and body weight variation between the taxa

- **Hypothesis 2.2:** There is no relationship between patterns of vertebral shape variation and body weight variation between the taxa

These hypotheses will be tested by examining the extent to which the grouping of taxa with regard to vertebral size and shape corresponds to a grouping of taxa with respect to body mass.

Hypothesis 3

It there are inter-specific differences in size and shape between the four hominoid taxa, hypothesis 3 will test the relationship between inter-specific differences in lumbar vertebral size and shape and locomotor repertoire which also relates to body weight transmission and trunk position. In terms of locomotor and weight bearing functions, humans are most different from the other taxa, given the unique locomotor adaptations of *Homo*. Within the great ape taxa, African apes are more similar in locomotor functions than is either to *Pongo*.

- **Hypothesis 3.1:** There is no relationship between patterns of vertebral size variation and locomotor differences between the taxa

- **Hypothesis 3.2:** There is no relationship between patterns of vertebral shape variation and locomotor differences between the taxa

If analyses of vertebral size and shape differences between taxa indicate that *Homo* is most distinctive, *Pongo* is also distinctive and the African apes are more similar to each other than to any other taxon, then the study will have falsified one or more of the above sub-hypotheses and it will have identified congruence between patterns of locomotion and patterns of shape and size variation.

Hypothesis 4

Phylogenetic analyses of the hominoid taxa in this study, based on molecular data, presently support the view that *Homo sapiens* and *Pan troglodytes* are sister taxa whose nearest relative is *Gorilla gorilla* with *Pongo pygmaeus* being most distantly related (see review earlier in thesis).

- **Hypothesis 4.1:** There is no relationship between patterns of vertebral size variation and the phylogenetic relationships between the taxa

- **Hypothesis 4.2:** There is no relationship between patterns of vertebral shape variation and the phylogenetic relationships between the taxa

These sub-hypotheses will be tested by comparing the clustering of taxa that arises from analyses of size and shape variability with the phylogenetic relationships between the same taxa.

Hypothesis 5

Thus far, the study is concerned with patterns of size and shape variation between taxa based on single lumbar vertebrae. However it is also of interest to consider how vertebral form varies along the lumbar vertebral column in each taxon, because this too, potentially relates to body weight, locomotor functions, and phylogenetic history. First, the study aims to identify any inter-specific differences in inter-segmental size and shape variation between the taxa.

- **Hypothesis 5:** There are no differences in patterns of lumbar inter-segmental shape variation between the taxa

This hypothesis will be tested by comparing patterns of lumbar inter-segmental shape variation between the taxa.

Hypothesis 6

If differences in patterns of lumbar inter-segmental size and shape variation are present between the taxa, then the study aims to assess the extent to which these are related to; (1) inter-specific difference in body weight (2) inter-specific differences in locomotor repertoire and so body weight transmission in relation to trunk position, and, (3) phylogenetic history

> **Hypothesis 6.1:** There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and body weight variation between the taxa
>
> **Hypothesis 6.2:** There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and inter-specific differences in locomotor repertoire
>
> **Hypothesis 6.3:** There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and phylogenetic history

4.3.2 Further aim

A further aim of the study - if hypothesis 5 is falsified - is to examine the ontogeny of differences in patterns of inter-segmental size and shape variation along the lumbar spine between the taxa. This is of interest because if these differences are present early in ontogeny it implies they are under strong genetic control, otherwise the later development of differences implies the influence of function in their ontogeny.

4.4. Materials and methods

4.4.1 Materials

The non-human primate sample in this study consists of dry vertebrae of an adult sample of 33 female and 24 male *Gorilla gorilla*, 24 female and 18 male *Pan troglodytes*, and 6 female and 6 male *Pongo pygmaeus* specimens. The adult modern human sample consists of 21 females and 25 males. It was drawn from a historic

European population as well as from contemporary populations from Europe, Asia, and Africa. For the study of ontogenetic allometry of the pattern of inter-segmental shape variation, a sample of subadult specimens, consists of 8 female and 8 male infants and 11 female and 5 male juveniles for *Gorilla gorilla* has been collected. The subadult sample of *Pan troglodytes* is represented by 10 female and 15 male infants and 9 female and 13 male juveniles. Subadult samples of *Pongo pygmaeus* and modern humans were difficult to access. Thus, these samples are small and the ratio of the sexes is unbalanced: the *Pongo pygmaeus* sample consists of one female and two male infants and one female and one male juvenile respectively. In the case of modern humans, there were only four male infants and four female juveniles available. Only individuals with complete vertebral columns free of pathological changes were selected. For all specimens, information on sex was provided by field and collection records.

The sub-adult samples are divided into the following broad age groups; infant, juvenile, and adult. The definitions of these age groups are based on dental development and the degree of closure of postcranial epiphyses (full description in Chapter II, materials and methods, p. 96). Briefly, specimens were considered adult if their postcranial skeleton is fully mature, meaning that all epiphyses are closed or closing thus visible in small traces only. The permanent dentition has to be fully developed, thus, 3rd molars and the canines are fully erupted and occluded. Juvenile specimens are characterized by partially closed limb bone and acetabular epiphyses. Their deciduous dentition is complete and at least one permanent tooth is already erupted. Specimens were considered infants if their limb bone as well as acetabular epiphyses were open and their deciduous dentition was in the process of completion. Based on these definitions, the human infant sample consists of two specimens only, aged 4.5 and 4.17 years respectively (Humphrey, 1998). Human juvenile specimens were estimated to have died aged 7, 7.8, 10.4, 16.5, 17.5, and 17.7 years of age.

4.5. Methods - general

For this study, the forms of the last five consecutive presacral vertebrae of each specimen in the sample were recorded as sets of 62 three-dimensional bony landmarks. The landmarks were chosen to reflect the detailed form of each vertebra, hence their high density. According to the definition by Bookstein (1991), the landmarks chosen for this study are either of type II (tips of anatomical structures) or type III (borders of

structures). For detailed information of data collection technique and a complete list of the landmarks used see Chapter II materials and methods.

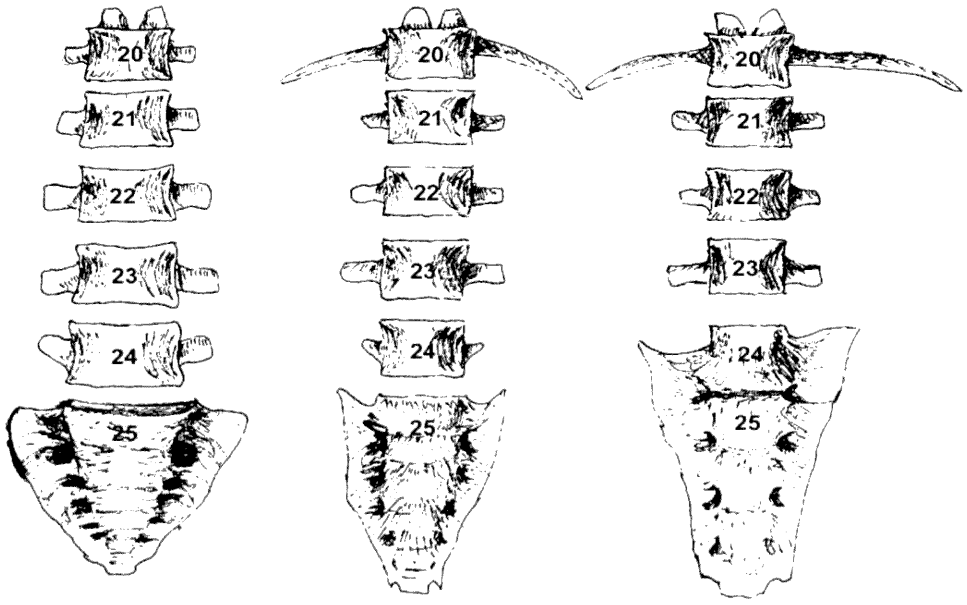
Statistical methods employed to analyse landmark data consisted of GPA/PCA. The landmark data was further analysed with step-wise discriminant analysis. Supplementary methods used for assessing levels of significance of inter-specific differences within the data consisted of Pearson's correlation coefficient, permutation test, and independent t-tests. For further details on all these statistical methods also refer to Chapter II, materials and methods.

4.5.1 The issue of comparing primate taxa with different numbers of lumbar vertebrae

How to compare the lumbar spine of primate taxa when the number of lumbar vertebrae varies intra – and more importantly inter-specifically, is a problem that has always challenged researchers conducting comparative morphological studies of the primate vertebral column. Since there is no one correct solution to this problem, ways around it usually depend on the particular questions a study addresses. Some authors define vertebral levels along the lumbar spine which allow the comparison of either functionally or phylogenetic equivalent vertebrae (Martelli and Schmid, 2003; Sanders, 1998; Sanders and Bodenbender, 1994). This approach is also employed in the present study.

Based on studies of vertebral numbers by Schultz (1961), Schultz and Straus (1945), Häusler et al. (2002), and Pilbeam (2004) the most common pattern of distribution of thoracic and lumbar vertebrae in humans and the two most common patterns in African great apes are illustrated in figure 4.2 (first presented in Chapter II, materials and methods, p 29, as figure 2.9 but repeated here for ease of reading). These patterns are used to define the vertebral comparison levels in figures 4.3 and 4.4. However, figure 4.2 illustrates the difference between modern humans and African great apes. *Pongo*, on the other hand, possesses on average only 23 instead of 24 presacral vertebrae (Benade, 1990; Schultz and Straus, 1945). Usually, there are only twelve *Pongo* thoracic vertebrae – as in modern humans (Häusler et al., 2002; Schultz and Straus, 1945). Therefore, *Pongo* lumbar vertebrae are not phylogenetically equivalent with the ones of African great apes. Yet functionally they can be aligned very well with the lumbar

vertebrae of African ape specimens with four lumbars. In order to facilitate the level-wise comparison of single lumbar vertebrae and because there are only twelve adult *Pongo* specimens in the sample, it was decided to treat the *Pongo* specimens are like African ape specimens with four lumbars.



Human with five lumbars **Ape with four lumbars** **Ape with three lumbars**

Figure 4.2 Distribution of thoracic, lumbar and sacral vertebrae in humans and African apes. Numbers derive from counting the vertebrae from the atlas (C1) towards the sacrum. Drawings are not true to scale, neither to natural size nor between the different specimens

Five comparison levels are defined along the lumbar spine. The first lumbar vertebra of humans is phylogenetically equivalent to the last thoracic vertebra of African great apes. Therefore, two vertebral comparison levels, labelled level 1, solution 1 and level 1, solution 2 are defined. Level 1, solution 1 acknowledges the functional equivalence of L1 of both modern humans and African apes. First lumbars are compared regardless of their phylogenetic background. In level 1, solution 2, the second lumbar of humans is compared to the first lumbars of all ape taxa. In this, the phylogenetically equivalent vertebrae are compared. Figure 4.3 shows level 1 solution 1 and levels 2 to 4.

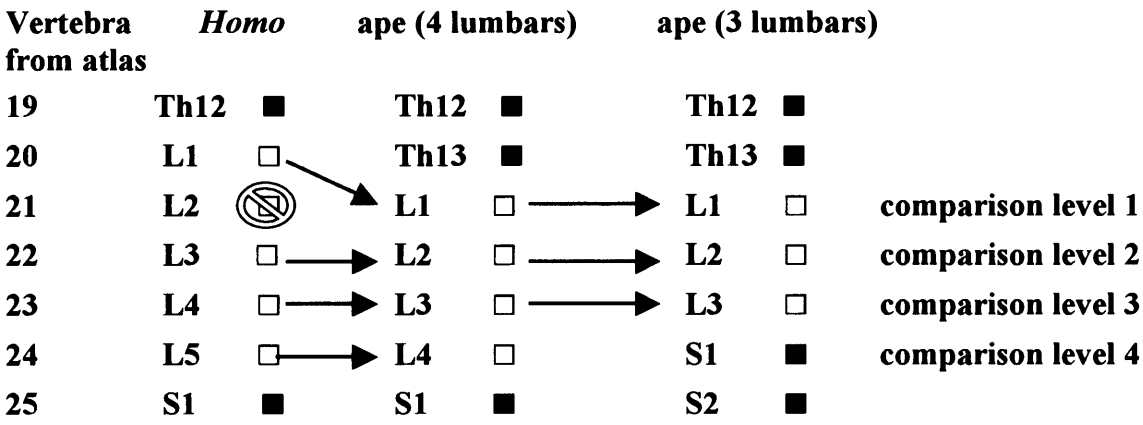


Figure 4.3 Definition of inter-specific comparison levels showing solution 1 for comparison level 1. Arrows link the vertebrae that are compared with each other. Crossed out vertebrae are not included into the comparison

Figure 4.4 on the other hand shows level 1 solution 2. In the African ape sample, the first three lumbars are phylogenetically equivalent since there are no differences in the number of thoracic vertebrae of specimens with three and four lumbars. L4 on the other hand, does not have an equivalently free lumbar vertebra in specimens with only three lumbar vertebrae (see figures 4.2 and 4.3). Therefore, in analysis of level 4, the latter were excluded.

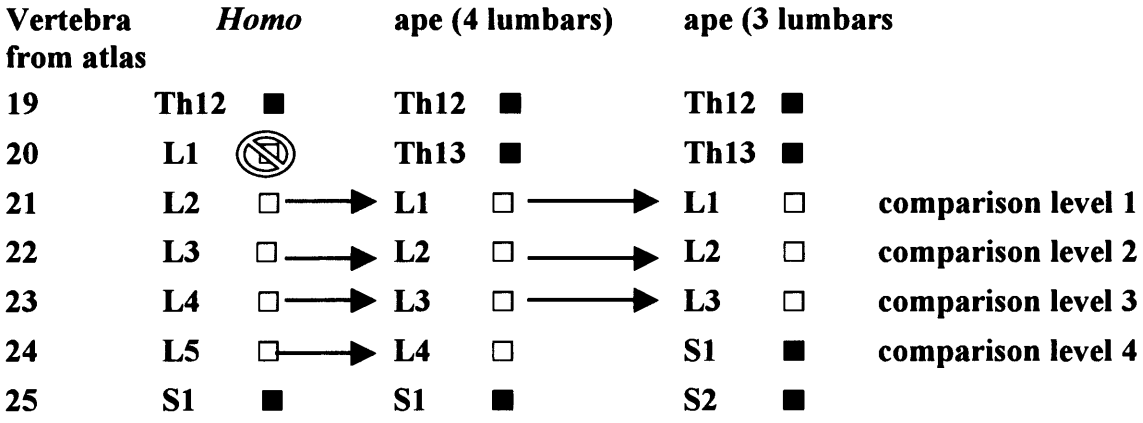


Figure 4.4 Definition of inter-specific comparison levels showing solution 2 for comparison level 1. Arrows link the vertebrae that are compared with each other. Crossed out vertebrae are not included into the comparison

Thus, the sample size of African apes is diminished by about 30% (*Gorilla* and *Pan*) in analysis of comparison level 4. Since sample sizes are large (57 adult *Gorilla gorilla* specimens and 42 *Pan troglodytes* specimens), samples consisting only of specimens

with four elements are considered large enough to yield statistically significant results. No problems arose for the samples of *Pongo*: all specimens have four lumbars.

4.5.2 Methods – operationalizing the testing of hypotheses 1 to 6.3

This study presents **seven analyses** to test the six hypotheses formulated previously as follows:

Hypothesis 1.1: There are no differences in vertebral centroid size between the four hominoid taxa in the study

This hypothesis is tested by comparing the vertebral centroid sizes of all pair-wise combinations of hominoid taxa at each vertebral comparison level (definition comparison levels see above). The significance of differences in vertebral centroid size between pairs of taxa is tested for with independent t-tests. The hypothesis will be falsified if **analysis 1** yields statistically significant differences in vertebral centroid size between the taxa in the study.

Hypothesis 1.2: There are no inter-specific differences in vertebral shape observed between the four hominoid taxa in this study

To test for inter-specific differences in vertebral shape between the taxa, Procrustes distances between shape configurations are calculated at each comparison level and for all pair-wise combinations of taxa. In **analysis 2** permutation tests are performed to calculate the significance of differences in vertebral shape between the taxa. This hypothesis will be **falsified** if statistically significant differences in vertebral shape are identified between the four hominoid taxa in the study.

The relationship between body weight variation and patterns of vertebral size variation will be tested for by hypothesis 2.1.

Hypothesis 2.1: There is no relationship between patterns of vertebral size variation and body weight variation between the taxa

The body weights are compiled from the literature (see table 4.1). Patterns of vertebral size variations result from **analysis 1** (see above). Hypothesis 2.1 will be **falsified** if there is a relationship between patterns of vertebral size variation and body weight variation between the taxa.

Hypothesis 2.2 tests for the presence or absence of relationships between body weight variation and patterns of vertebral shape variation between the taxa:

Hypothesis 2.2: There is no relationship between patterns of vertebral shape variation and body weight variation between the taxa

The variation in body weight between the taxa is compiled from the literature (see table 4.1). Patterns of vertebral shape variation result from **analysis 2** (see above). Hypothesis 2.2 will be **falsified** if there is a relationship between patterns of vertebral shape variation and body weight variation between the taxa.

Sub-hypotheses 3.1 and 3.2 drive the investigation of relationships between vertebral size and shape and differences in locomotor repertoire between the taxa.

Hypothesis 3.1: There is no relationship between patterns of vertebral size variation and locomotor differences between the taxa

To test hypothesis 3.1 (size), results, provided by **analysis 1** (the patterns of vertebral size variation), will be compared with the known (from the literature) differences in locomotor repertoire between the taxa. From these it is expected that African apes are most similar in size, *Pongo* is more similar to the African apes, and humans are most distinct from all great apes - if size reflects locomotor repertoires. Hypothesis 3.1 will be **falsified** if there is a relationship between vertebral size variation and locomotor differences between the taxa.

Hypothesis 3.2: There is no relationship between patterns of vertebral shape variation and locomotor differences between the taxa

For testing hypothesis 3.2 (shape), the differences in locomotor repertoire are compared to the patterns of vertebral shape variation between the taxa. The latter are investigated

with **analyses 3** and **4**. In analysis 3, shape data is analysed with GPA/PCA to investigate differences in shape between all specimens of all taxa at all vertebral comparison levels. Step-wise discriminant analysis will be performed on the PCs yielded by GPA/PCA to identify the PCs summarizing differences in shape which best discriminate between the taxa. Plots of these PC will visualize the discrimination (differences in shape) between the taxa. Analysis 4, instead of analysing complete samples, investigates species mean shapes of all four hominoid taxa at each vertebral comparison level. Since analyzing whole samples results in a high dimensional shape space and differences between taxa are to some extent obscured by differences in intra-specific shape variation, the analysis of species mean shapes reduces dimensionality and allows direct comparison of differences in shape between species means. The methods used are the same as in analysis 3 – the data is analysed with GPA/PCA. Plots of PCs are presented. Differences in shape between the mean species shapes are visualized using transformation grids with distortions thereof, representing differences in shape. The grid distortions are calculated with thin spline techniques. Hypothesis 3.2 will be **falsified** if there is a relationship detected between the patterns of vertebral shape variation and locomotor differences between the taxa.

Sub-hypotheses 4.1 and 4.2 are tested to investigate the presence or absence of relationships between phylogenetic relationships and patterns of variation of lumbar vertebral size and shape between the hominoid taxa in the study.

Hypothesis 4.1: There is no relationship between patterns of vertebral size variation and the phylogenetic relationships between the taxa

To test this hypothesis, phylogenetic relationships between the taxa are compared with vertebral size variations. The phylogenetic relationships employed are presented in the introduction and follow the results of studies of comparative molecular biology between the four hominoid taxa in the study (reviewed in Chapter I). Briefly, they state that modern *Homo sapiens* is the sister taxa of *Pan*. *Gorilla* is the next living relative to both of them and *Pongo* is the next living relative to all three. Patterns of vertebral size variation at each comparison level result from **analysis 1** (see above). Hypothesis 4.1 is **falsified** if there is a relationship between patterns of vertebral size variation and phylogenetic relationships between the taxa.

Hypothesis 4.2: There is no relationship between patterns of vertebral shape variation and the phylogenetic relationships between the taxa

Here, the same phylogenetic relationships are compared as used to test hypothesis 4.1. The patterns of shape variations at each comparison level result from **analysis 5**. UPGMA phenograms are computed at each vertebral comparison level to analyse distances between mean shapes of all four hominoid taxa. These phenograms are compared to the commonly accepted phylogenetic relationships. The hypothesis is falsified if there is a relationship between the patterns of vertebral shape variation and the phylogenetic relationships between the taxa.

Hypotheses 1 to 4 investigate differences in lumbar vertebral size and shape in relation to several factors (inter-specific differences in body weight, locomotor repertoires, and phylogenetic relationships). Hypothesis 5, on the other hand, is tested to discover possible differences in patterns of size and shape variation along the lumbar spine as a whole.

Hypothesis 5: There are no differences in patterns of lumbar inter-segmental size and shape variation between the taxa

Patterns of lumbar inter-segmental size and shape variation are obtained in **analysis 6**. Methods employed are GPA/PCA, used on species mean shape data of all lumbar vertebrae and all taxa. The results are presented in two and three dimensional PC plots which facilitate the visualization of differences in inter-segmental shape variation patterns along the lumbar spine in all four hominoid taxa in the study. Hypothesis 5 is **falsified** if there are differences in patterns of lumbar inter-segmental shape variation between the taxa.

If hypothesis 5 is falsified, sub-hypotheses 6.1 to 6.3 are tested for the presence or absence of relationships between inter-specific differences in patterns of inter-segmental shape variation along the spine and inter-specific differences in body weight, locomotor repertoires, and phylogenetic relationships.

Hypothesis 6.1: There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and body weight variation between the taxa

This hypothesis is tested by comparing differences in body weight with the patterns of inter-segmental shape variation and the patterns of inter-segmental size variation along the lumbar spine. Differences in body weight between the taxa are summarized in table 4.1 and are compiled from the literature. Patterns of inter-segmental size and shape variation are produced and compared in **analysis 6**. The hypothesis is falsified if there is a relationship between differences in patterns of inter-segmental size or shape variation and body weight differences between the taxa.

Hypothesis 6.2: There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and inter-specific differences in locomotor repertoire

This hypothesis is tested by comparing differences in locomotor repertoire with the patterns of inter-segmental size and shape variation along the lumbar spine. Differences in locomotor repertoire were compiled from the literature. Briefly, modern humans are very different from all other taxa in this study, since they exclusively walk bipedally. The locomotor repertoires of *Gorilla* and *Pan* resemble each other the most. *Pongo* is different from both modern humans and great apes. Differences in locomotor repertoire will be compared with the results from **analysis 6** (patterns of inter-segmental size and shape variation along the lumbar spine between the taxa). The hypothesis is **falsified** if there is a relationship between patterns of inter-segmental size or shape variation and differences in locomotor repertoires between the taxa.

Hypothesis 6.3: There is no relationship between patterns of inter-segmental size and shape variation along the lumbar spine between the taxa and phylogenetic history

Here, phylogenetic relationships are compared between the taxa with patterns of inter-segmental size and shape variation along the lumbar spine. The same pattern of phylogenetic relationships is employed as for testing analyses 4.1 and 4.2 (see above). These are compared with the patterns of inter-segmental size and shape variation from

analysis 6. The hypothesis is **falsified** if there is a relationship between patterns of inter-segmental shape variation and phylogenetic relationships between the taxa.

If hypothesis 5 is falsified, the ontogeny of differences in patterns of inter-segmental shape variation along the lumbar spine between the taxa will be further investigated. In this case, a sample of immature specimens of each taxon will be divided into a younger (infants) and an older (juvenile) sub-sample. In **analysis** 7, each sub-sample will be analysed with GPA/PCA of the mean species shape of each lumbar vertebra. Plots of PCs will be provided for visualization of inter-specific differences in patterns. Patterns of inter-segmental shape variation and differences therein between the taxa will be compared with the patterns of inter-segmental shape variation of the adult sample (analysis 6). Results from this comparison will help to determine if differences in inter-segmental shape variation along the lumbar spine observed in the adult sample are visible early (infant) in postnatal ontogeny (under strong genetic control) or appear later (juvenile) in ontogeny (influenced considerably by function).

4.6 Results

4.6.1 Analysis 1, assessing inter-specific differences in vertebral size

In table 4.2, the mean vertebral centroid sizes of sex means at each lumbar vertebral level are tabulated for all hominoids. The table also displays the 95% confidence limits (= 2 sds). These vertebral centroid sizes and pair-wise independent t-tests were used to assess significances of apparent differences in size between modern taxa at different vertebral levels. They also serve to underpin further analysis of differences in vertebral shape. Table 4.3 summarizes the results of inter-specific centroid size comparisons at all comparative levels between all taxa in the study. There are significant differences (even with Bonferroni correction) in vertebral centroid size observed between *Gorilla* and *Pan* and *Gorilla* and *Pongo* as well as between *Homo sapiens* and *Pan* and *Homo sapiens* and *Pongo*. However, significant differences in centroid size between *Homo sapiens* and *Gorilla* are only identified for the comparison of the first and last lumbar vertebrae. The values indicate that modern humans have significantly smaller first lumbar vertebrae than *Gorilla*. On the other hand, the last lumbars of modern humans are significantly larger than the ones of *Gorilla*.

Taxon	L1	L2	L3	L4	L5
Gorilla gorilla ♂	**9.3688** ± 1.1328	**9.2323** ± 1.5442	**9.2997** ± 0.9836	**8.8452** ± 1.0204	
	(1sd = 0.5664)	(1sd = 0.7721)	(1sd = 0.4918)	(1sd = 0.5102)	
Gorilla gorilla ♀	**7.6454** ± 0.8672	**7.6523** ± 0.8134	**7.5803** ± 0.9276	**7.2023** ± 0.6836	
	(1sd = 0.4336)	(1sd = 0.4067)	(1sd = 0.4638)	(1sd = 0.3418)	
Pan troglodytes ♂	**6.8021** ± 0.6266	**7.1760** ± 0.6820	**7.0925** ± 0.6026	**6.7620** ± 0.4886	
	(1sd = 0.3133)	(1sd = 0.341)	(1sd = 0.3013)	(1sd = 0.2443)	
Pan troglodytes ♀	**6.5234** ± 0.6252	**6.7448** ± 0.5614	**6.7427** ± 0.270	**6.5495** ± 0.8864	
	(1sd = 0.3126)	(1sd = 0.2807)	(1sd = 0.1350)	(1sd = 0.4432)	
Pongo pygmaeus ♂	**7.4098** ± 0.5798	**7.5786** ± 0.5468	**7.4614** ± 1.4266	**7.4670** ± 0.7958	
	(1sd = 0.2899)	(1sd = 0.2734)	(1sd = 0.7133)	(1sd = 0.3979)	
Pongo pygmaeus ♀	**6.2578** ± 0.3758	**6.3010** ± 0.6238	**6.3510** ± 0.688	**6.2278** ± 0.284	
	(1sd = 0.1876)	(1sd = 0.3119)	(1sd = 0.3440)	(1sd = 0.1420)	
Homo sapiens ♂	**7.9714** ± 0.8966	**8.3378** ± 0.8614	**8.6042** ± 0.959	**8.7382** ± 0.546	**9.0939** ± 1.0134
	(1sd = 0.4483)	(1sd = 0.4307)	(1sd = 0.4795)	(1sd = 0.2730)	(1sd = 0.5067)
Homo sapiens ♀	**7.3488** ± 0.8272	**7.6983** ± 0.7726	**7.9049** ± 0.7662	**7.9633** ± 0.786	**8.3327** ± 0.8578
	(1sd = 0.4136)	(1sd = 0.3863)	(1sd = 0.3831)	(1sd = 0.3930)	(1sd = 0.4289)

Table 4.2 Tabulation of centroid sizes and the 95% confidence limit (= 2sds) of all modern taxa. First line = sexes means centroid size and 95% confidence limit, second line = standard deviation

Comparison level *Homo* vs. apes Apes vs. apes	***Homo sapiens*** ***Gorilla gorilla***	***Homo sapiens*** ***Pan troglodytes***	***Homo sapiens*** ***Pongo pygmaeus***	***Pan troglodytes*** ***Gorilla gorilla***	***Gorilla gorilla*** ***Pongo pygmaeus***	***Pan troglodytes*** ***Pongo pygmaeus***
L1-L1	**-0.6618**	**1.0340***	**0.7955***	**-1.6958**	**1.4573***	-0.2385
L1-L1	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	p=0.136
L1-L2	-0.3015	**1.3943**	**1.1558***			
-	p=0.069	**p=0.001**	**p=0.001**			
L2-L3	-0.07253	**1.3621**	**1.3519***	**-1.4347**	**1.4245***	0.2368
L2-L2	p=0.655	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	p=0.967
L3-L4	0.1259	**1.5026**	**1.4878***	**-1.3767**	**1.3618***	-0.01483
L3-L3	p=0.426	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	p=0.955
L4-L5	**0.7066**	**2.0980**	**1.9064***	**-1.3914**	**1.1998**	-0.1917
L4-L4	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	p=0.269

Table 4.3 Inter-specific differences in vertebral centroid size, significance tested with independent t-tests. Summary of the results from the pair-wise calculated independent t-tests between all modern taxa and centroid size at all comparison levels. First line shows mean differences in centroid size (in cm). Second line shows values (p-value) of significance for differences in mean centroid size. Asterisks (*) marks test statistics, for which the assumption of "equal variances assumed" is applicable (evaluated with Levene's test). Values significant at the level $p < 0.001$ are highlighted. The tests are even significant taking into account Bonferroni corrections (significance tests n = 27, familywise error = 75.0%, p-Bonferroni corrected = 0.001)

The comparison of *Pan* and *Pongo* vertebrae did not indicate significant differences in centroid size between the two taxa at any comparison level. However, when the sexes are analysed separately, because *Pongo* is highly sexually dimorphic whereas *Pan* is not, then results indicate that male *Pongo* vertebral centroid size is significantly larger than that of male *Pan* one (see table 4.4).

Comparison level	*Pan troglodytes*, females *Pongo pygmaeus*, females	*Pan troglodytes*, males *Pongo pygmaeus*, males	*Gorilla gorilla* females *Pongo pygmaeus* males
L1-L1	0.2657* p=0.119	**-0.6077*** **p=0.001**	0.2356* p=0.252
L2-L2	**0.4438*** **p=0.004**	**-0.4026*** **p=0.014 #**	0.0737* p=0.699
L3-L3	**0.4094*** **p=0.019 #**	**-0.6730*** **p=0.001**	-0.1852* p=0.441
L4-L4	0.3217* p=0.135	**-0.7050*** **p=0.000**	-0.2647* p=0.132

Table 4.4 Centroid size differences between *Pongo pygmaeus* and other apes, separated by sex. First line shows mean differences in centroid size (in cm), second shows p-values for differences in mean centroid size. * indicate test statistics, for which the assumption of "equal variances assumed" is applicable (evaluated with Levene's test). Values significant at the level $p < 0.01$ and $p>0.05$ are highlighted. Note that a Bonferroni correction renders the tests marked '#' insignificant (significance tests n = 12, familywise error = 46 %, p-Bonferroni corrected = 0.004)

Results from the comparison of female *Pan* and *Pongo* samples are mixed: significant differences in centroid size between females are observed at the vertebral comparison levels 2 and 3 (or 2 alone if the Bonferroni correction is applied), indicating that female orang-utans have somewhat smaller vertebrae than female chimpanzees. At comparison levels 1 and 4, the differences in centroid size between the two female samples are non-significant. In order to establish to what degree body weight alone might impact on the size of vertebrae, further analyses with *Pongo* (males) and *Gorilla* (females) were conducted because both are more or less equivalent in body weight (see table 4.1). Results summarized in table 4.4 show no significant differences in vertebral centroid size between male *Pongo* (= female *Gorilla* weight) and female *Gorilla* lumbar vertebrae at all comparison levels. Therefore, differences in overall body weight between the great ape taxa are reflected in differences in centroid size of the lumbar

vertebrae when sexual dimorphism is taken into account. However in the comparison of *Homo sapiens* and *Gorilla*, functional as well as body weight differences seem to have an effect. Thus the first lumbar vertebra is significantly smaller and the last one is significantly larger, presumably reflecting functional differences which predominate over body mass differences (*Gorilla* is consistently larger than *Homo sapiens*).

Finally, mean differences in vertebral centroid size between all pairs of taxa were computed and used to produce the phenogram shown in figure 4.5 using the UPGMA method of clustering. The phenogram indicates that humans are as similar to *Gorilla* in mean vertebral size as are *Pan* and *Pongo*.

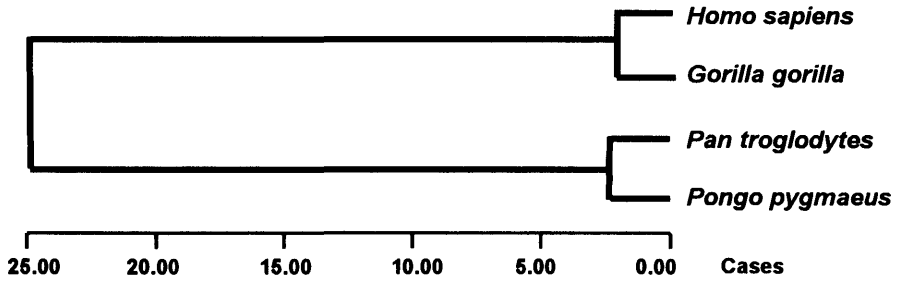


Figure 4.5 UPGMA Phenogram based on mean differences in vertebral centroid size between all taxa in the study

4.6.2 Analysis 2, assessing inter-specific differences in vertebral shape

An assessment of differences in vertebral size between the taxa is followed by an assessment of differences in vertebral shape between the taxa. Thus, permutation tests were used to assess the significance of Procrustes distances between vertebral shape configurations of all taxa, at each vertebral comparison level. Results indicate that all hominoid taxa in this study significantly differ in lumbar vertebral shape from each other (table 4.5). The same applies even after Bonferroni correction.

Comparison level *Homo* vs. apes Apes vs. apes	***Homo sapiens*** ***Gorilla gorilla***	***Homo sapiens*** ***Pan troglodytes***	***Homo sapiens*** ***Pongo pygmaeus***	***Gorilla gorilla*** ***Pan troglodytes***	***Gorilla gorilla*** ***Pongo pygmaeus***	***Pan troglodytes*** ***Pongo pygmaeus***
L1-L1	**0.2139**	**0.1846**	**0.1964**	**0.1138**	**0.1201**	**0.1492**
L1-L1	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**
L1-L2	**0.2165**	**0.1786**	**0.2080**			
-	**p=0.001**	**p=0.001**	**p=0.001**			
L2-L3	**0.2185**	**0.1226**	**0.2129**	**0.1839**	**0.1453**	**0.1406**
L2-L2	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**
L3-L4	**0.2179**	**0.1766**	**0.2014**	**0.1068**	**0.1357**	**0.1386**
L3-L3	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**
L4-L5	**0.2717**	**0.2381**	**0.2434**	**0.0955**	**0.1538**	**0.1382**
L4-L4	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**	**p=0.001**

Table 4.5 Differences in vertebral shape between recent hominoid taxa. Differences in shape are represented by Procrustes distances between all possible pairs of taxa at each comparison level. Permutation tests are employed to estimate significance of Procrustes distances. First line: permutation distances (in cm), second line: p-values of significance of permutation distances. Values significant at the level $p < 0.01$ are highlighted. These are even significant taking into account Bonferroni corrections (significance tests n = 27, familywise error = 75.0%, p-value Bonferroni corrected = 0.001)

Modern humans are most different in shape from all other hominoid taxa and the differences in shape are most marked at comparison level 4 (last lumbars). The smallest differences in shape are observed between *Gorilla* and *Pan*, and the smallest differences here are seen between the last lumbars. Comparing hominoid body weights presented in table 4.1 with these differences in shape (table 4.5) is apparent that there is no strong relationship between differences in body weight and differences in vertebral shape. Thus *Gorilla* and *Pan* differ greatly in body weight but little in vertebral shape while humans and *Pongo* differ little in body weight but greatly in vertebral shape.

4.6.3 Analysis 3, exploring inter-specific differences in vertebral shape between samples of specimens of each taxon

Patterns of shape variation between the taxa are explored through GPA/PCA. Scatter plots of PCs extracted from GPA/PCA analyses on the total sample are displayed in figure 4.6 and 4.7. Results from analysis 2 (table 4.5) are mirrored in these PC plots and are consistent with them at all comparison levels. Differences in overall lumbar vertebral shape are largest between modern humans and the great apes. These differences in shape between humans and all great apes are most pronounced on PC1 (summarizing between 33.9% and 43.5% of the total shape variation). At comparison levels 1 (both solutions) through to level 3, according to step-wise discriminant analysis, PC2 consistently separates the small African ape *Pan* from the large bodied apes *Gorilla* and *Pongo* (figure 4.6). At comparison level 4 (last lumbar), however, the most powerful separator of small vs. large apes is PC5, summarizing 3.5% of the total shape variation with in the sample (see figure 4.6). In figure 4.8, plots of PCs are shown which summarize most differences in shape between African and Asian apes. At comparison levels 1 (solution 1), the best discriminator between the Asian and African apes is PC4 (5.1% TSV), whereas at comparison levels 1 (solution 2) through to level 3, this is PC3 (summarizing between 5.3% and 6.8% of the TSV). Again, comparison level 4 (last lumbars) is very different from the other comparison levels. Here, PC2 is the strongest discriminator between the Asian and African apes, summarizing 6.2% of the TSV (see figure 4.7).

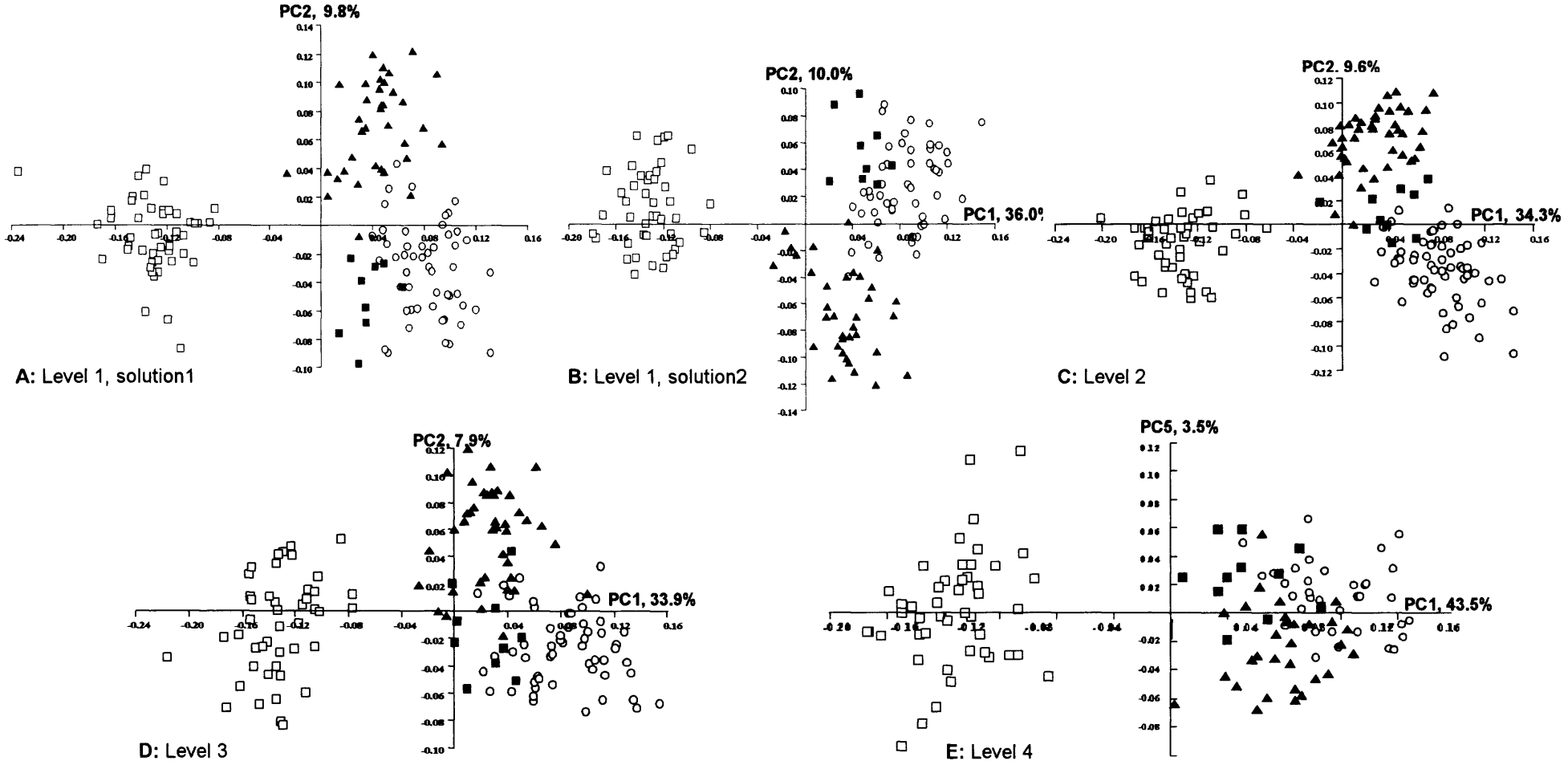


Figure 4.6 Scatter plots of PC1 vs. PC2, at all comparison levels, extracted from full modern samples. Plots summarize inter-specific differences in shape between *Homo sapiens* and all great apes along axis of PC1 **(A to E)**. Shape differences between the large bodied apes *Gorilla gorilla* and *Pongo pygmaeus* and the smaller ape *Pan troglodytes* seen along axis of PC 2 **(A to D)** and 5 **(E)**. □ = *Homo sapiens*, ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

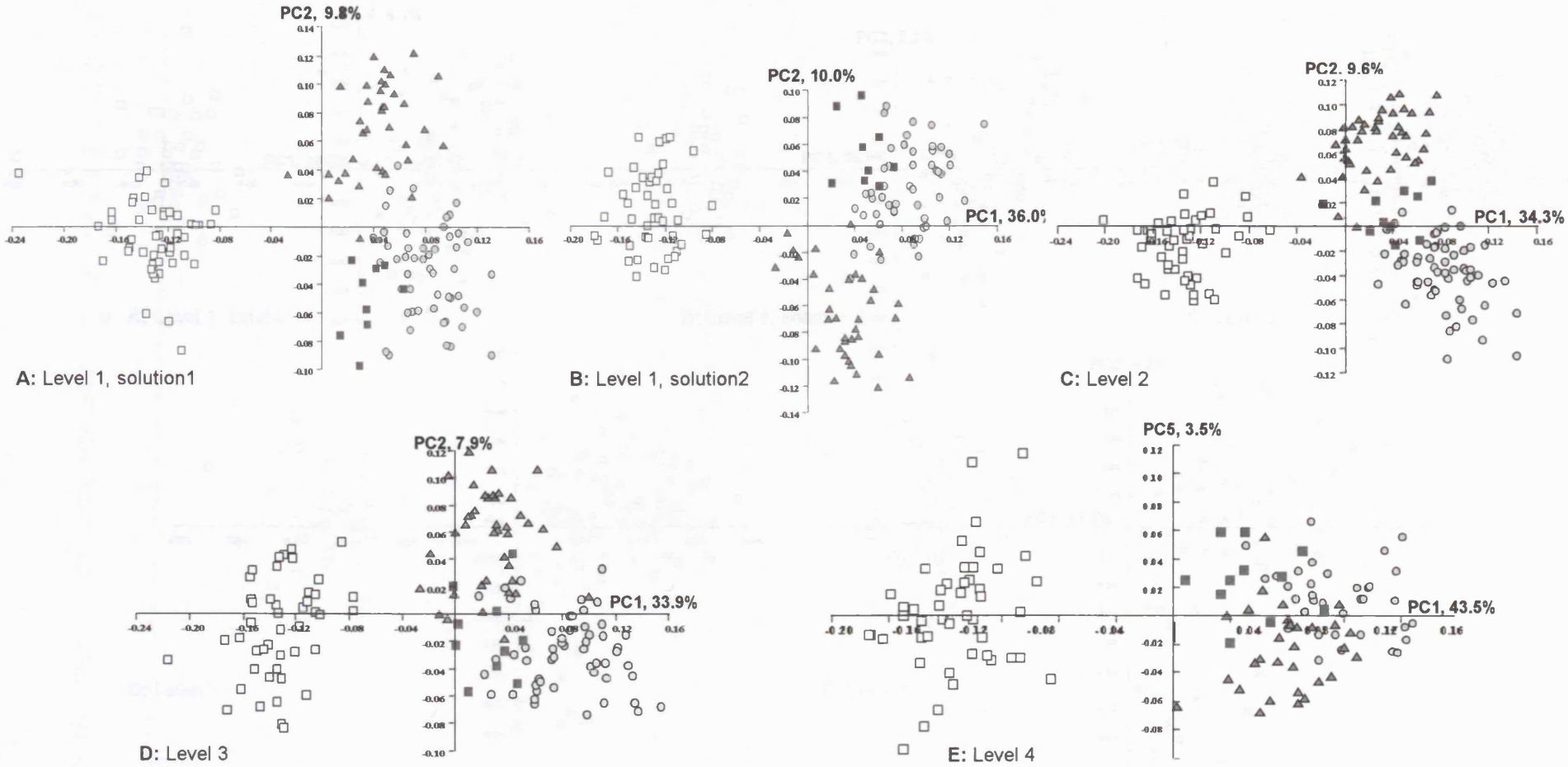


Figure 4.6 Scatter plots of PC1 vs. PC2, at all comparison levels, extracted from full modern samples. Plots summarize inter-specific differences in shape between *Homo sapiens* and all great apes along axis of PC1 **(A to E)**. Shape differences between the large bodied apes *Gorilla gorilla* and *Pongo pygmaeus* and the smaller ape *Pan troglodytes* seen along axis of PC 2 **(A to D)** and 5 **(E)**. □ = *Homo sapiens*, ◌ = *Gorilla gorilla*, △ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

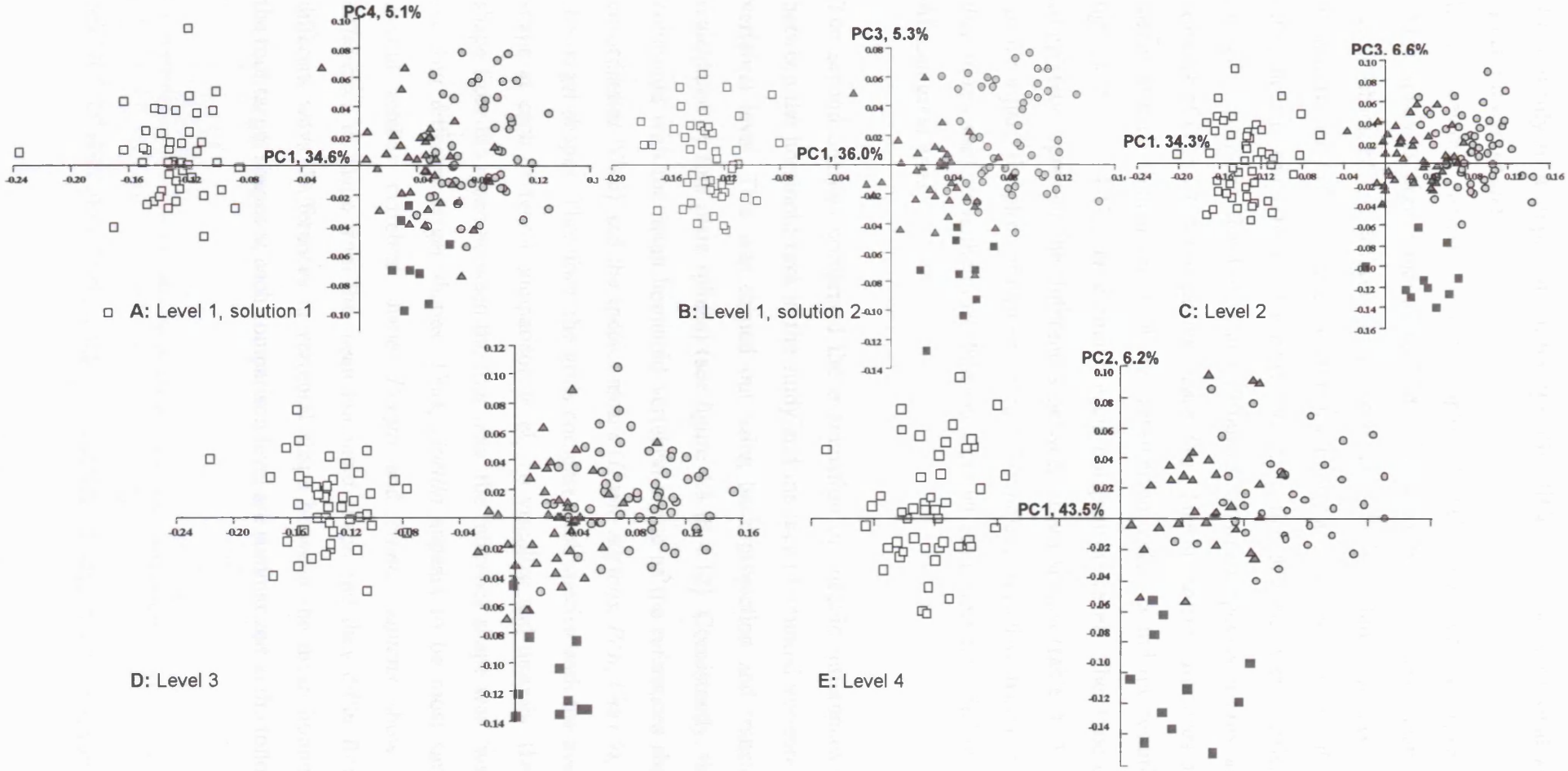


Figure 4.7 Scatter plots of PC1 vs. PC2, at all comparison levels, extracted from full modern samples. Plots summarize inter-specific differences in shape between *Homo sapiens* and all great apes along axis of PC1 **(A to E)**. Discrimination between the African apes *Gorilla gorilla* and *Pan troglodytes* and the Asian ape *Pongo pygmaeus* is summarized along PCs 2, 3, and 4 **(D, B/C**, and **1)**. □ = *Homo sapiens*, ◌ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

4.6.4 Analysis 4 exploring inter-specific differences in vertebral shape between species mean shapes

In the previous analyses, whole samples of each taxon were analysed. The resulting shape space is high dimensional and differences between mean shapes are to some extent obscured by differences between individuals within each taxon (intra-specific variation). In order to reduce dimensionality and to be able to directly compare differences in shape between species means, further analyses were carried out. The first analysis calculates the Procrustes distances between species means and the second consists of GPA/PCA on species means data. The Procrustes distances between species means at each comparison level are presented in table 4.6 and the resulting PC plots in figures 4.8 to 4.12, representing each comparison level. The Procrustes distances completely represent the differences between mean shapes (table 4.6). These and, for the most part, the plots of figures 4.8 to 4.12, indicate for all vertebral comparison levels that *Homo sapiens* is the most different from all other taxa followed by *Pongo* and the African great apes.

The second analysis comprised the examination of specific differences in mean shape between the hominoid taxa in the study and the mean hominoid vertebral shape at each vertebral level. This was carried out using back projection and transformation grids (calculated by thin plate splines) (see figure 4.8 to 4.12). Consistently, these grids were computed with the mean hominoid vertebral shape as the references shape (located at co-ordinates 0/0/0) and the species means (*Homo sapiens, Pan*, *Gorilla*, and *Pongo*) as the target shapes. Therefore, the grids compare each species with the average hominoid shape at each vertebral comparison level. To visualize and describe the differences in shape from the mean between the four taxa, the reference shape was "warped" towards the four different target shapes. Thus, *Gorilla* appears to be most similar to *Pan* in overall lumbar vertebral shape. *Pongo* and *Homo sapiens* show more marked differences in shape from the mean hominoid shape and they differ from the mean in different ways. Differences in vertebral shape between the mean hominoid shape and the four target shapes at each comparison level are summarized in the following section.

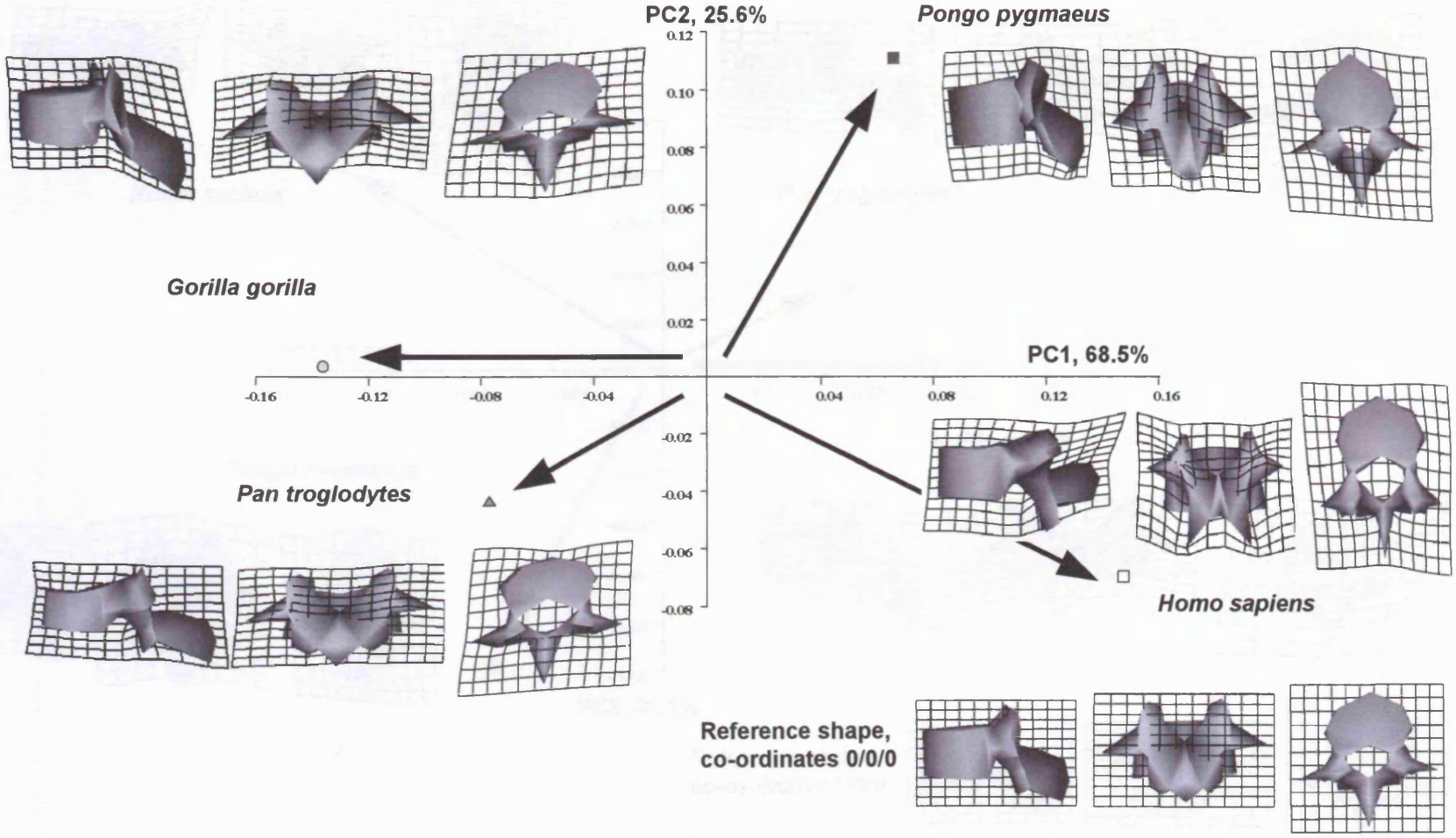


Figure 4.8 Scatter plot of PC1 vs. PC2, extracted from vertebral level means of modern taxa at comparison level 1, solution 1. Reference shape = Mean hominoid shape calculated from all four taxa and located at coordinates 0/0/0); target shapes = taxon mean shapes of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior and superior views (left to right). Grid positions indicate position of greatest grid distortion. □ = *Homo sapiens*, ☼ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

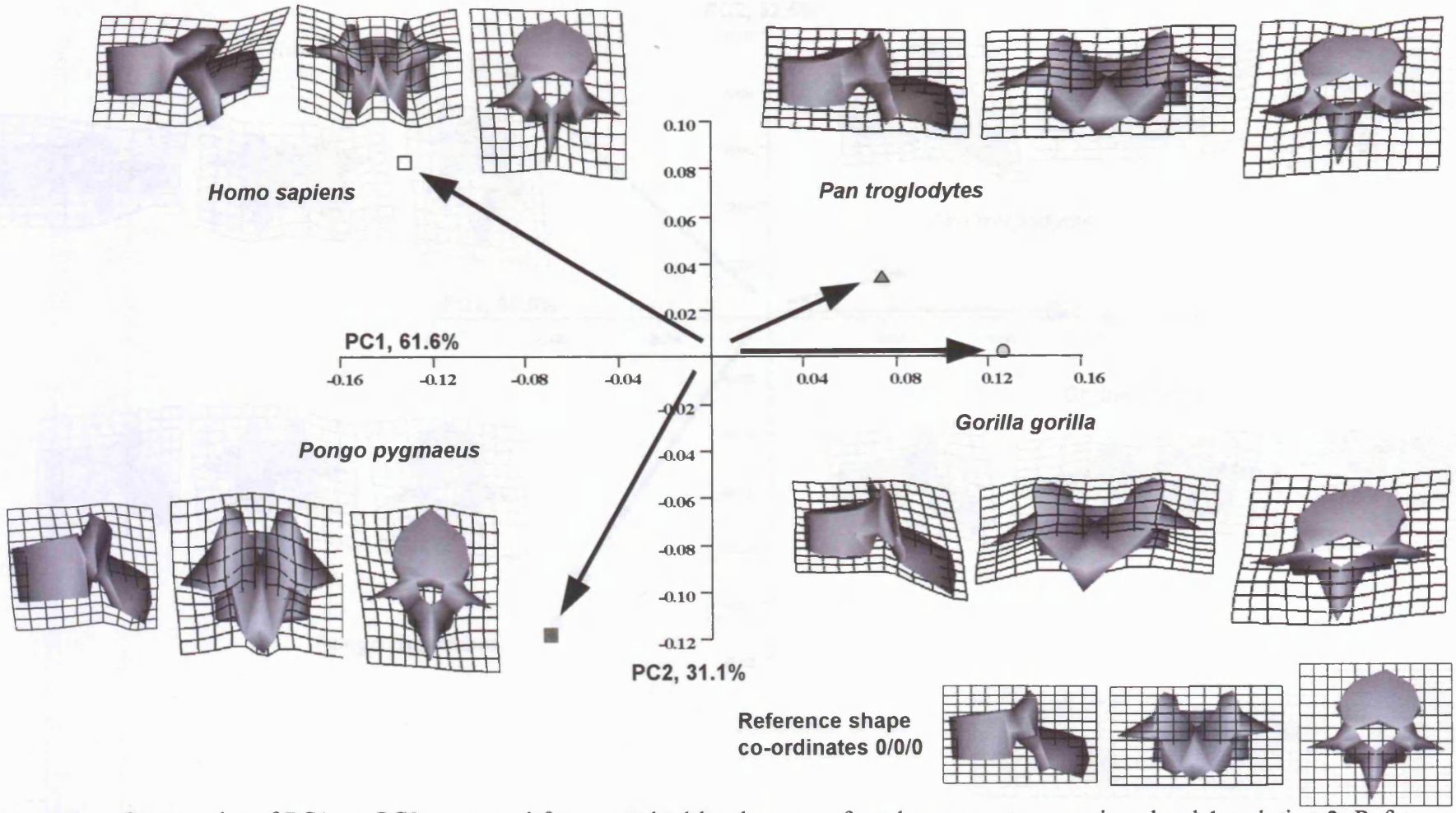


Figure 4.9 Scatter plot of PC1 vs. PC2, extracted from vertebral level means of modern taxa at comparison level 1, solution 2. Reference shape = Mean hominoid shape calculated from all four taxa and located at coordinates 0/0/0); target shapes = taxon mean shapes of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior and superior views (left to right). Grid positions indicate position of greatest grid distortion. □ = *Homo sapiens*, ○ = *Gorilla gorilla*, △ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

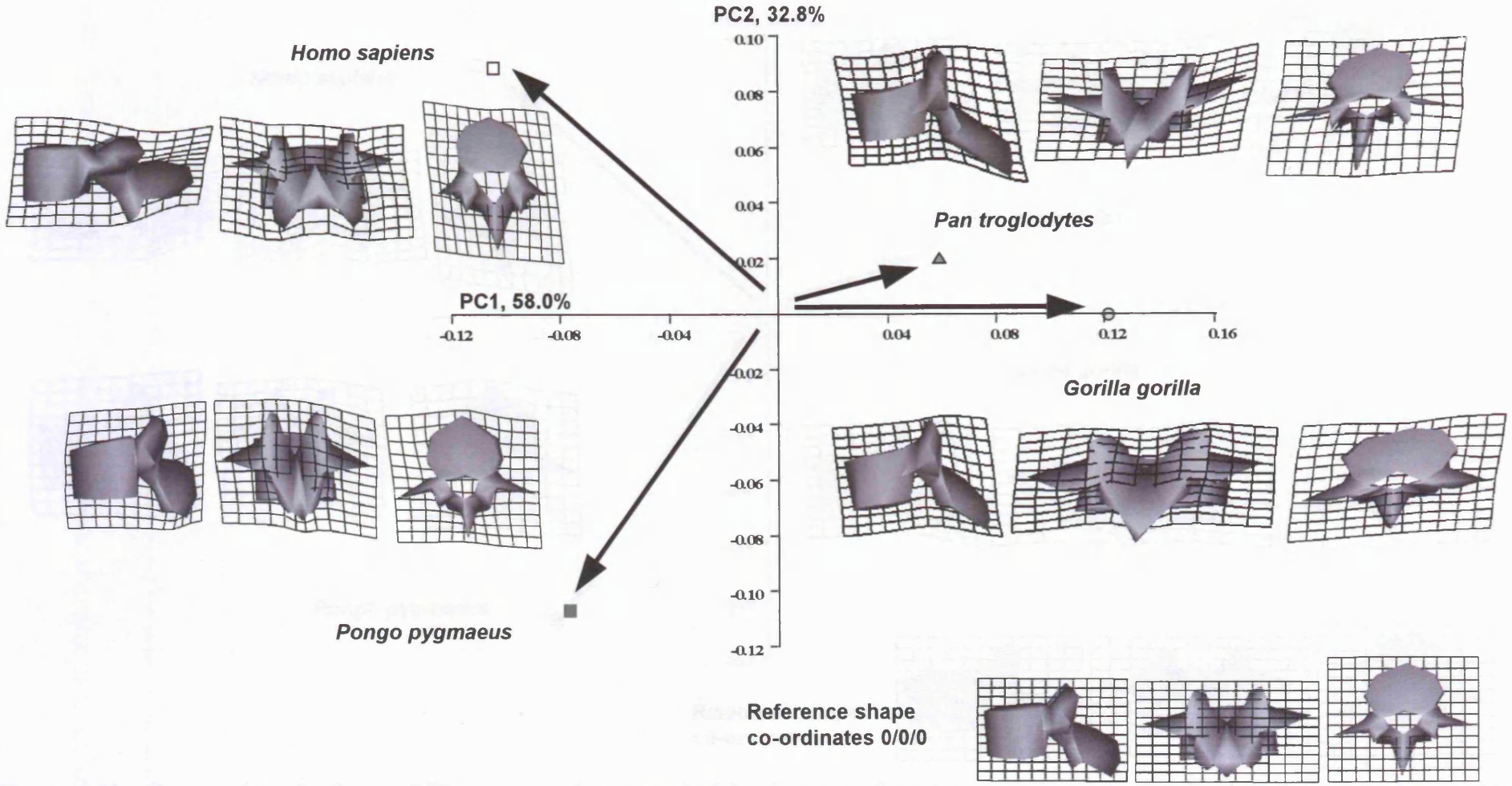


Figure 4.10 Scatter plot of PC1 vs. PC2, extracted from vertebral level means of modern taxa at comparison level 2. Reference shape = Mean hominoid shape calculated from all four taxa and located at coordinates 0/0/0); target shapes = taxon mean shapes of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior and superior views (left to right). Grid positions indicate position of greatest grid distortion. □ = *Homo sapiens*, ○ = *Gorilla gorilla*, △ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

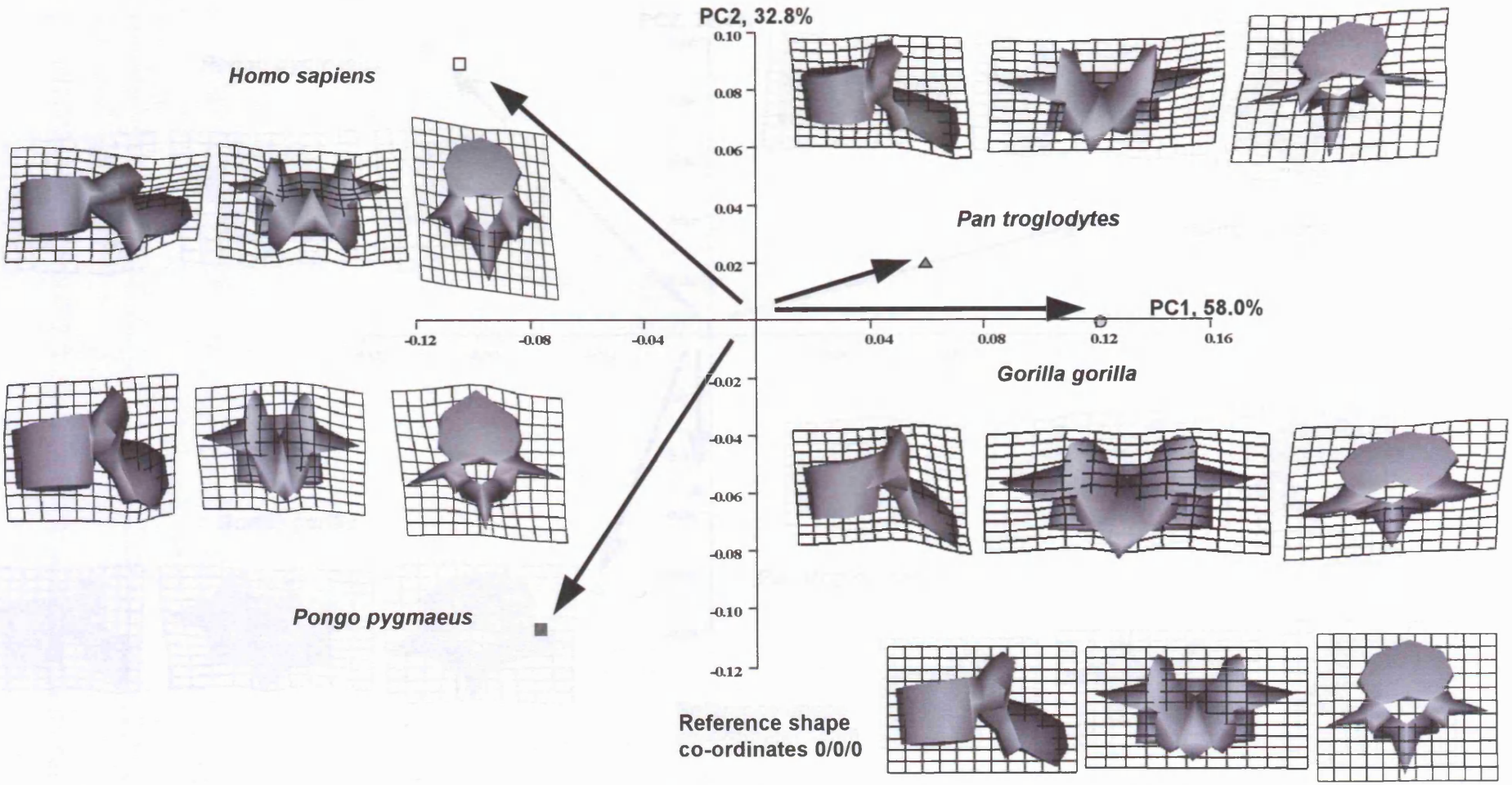


Figure 4.11 Scatter plot of PC1 vs. PC2, extracted from vertebral level means of modern taxa at comparison level 3. Reference shape = Mean hominoid shape calculated from all four taxa and located at coordinates 0/0/0); target shapes = taxon mean shapes of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior and superior views (left to right). Grid positions indicate position of greatest grid distortion. □ = *Homo sapiens*, ○ = *Gorilla gorilla*, △ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

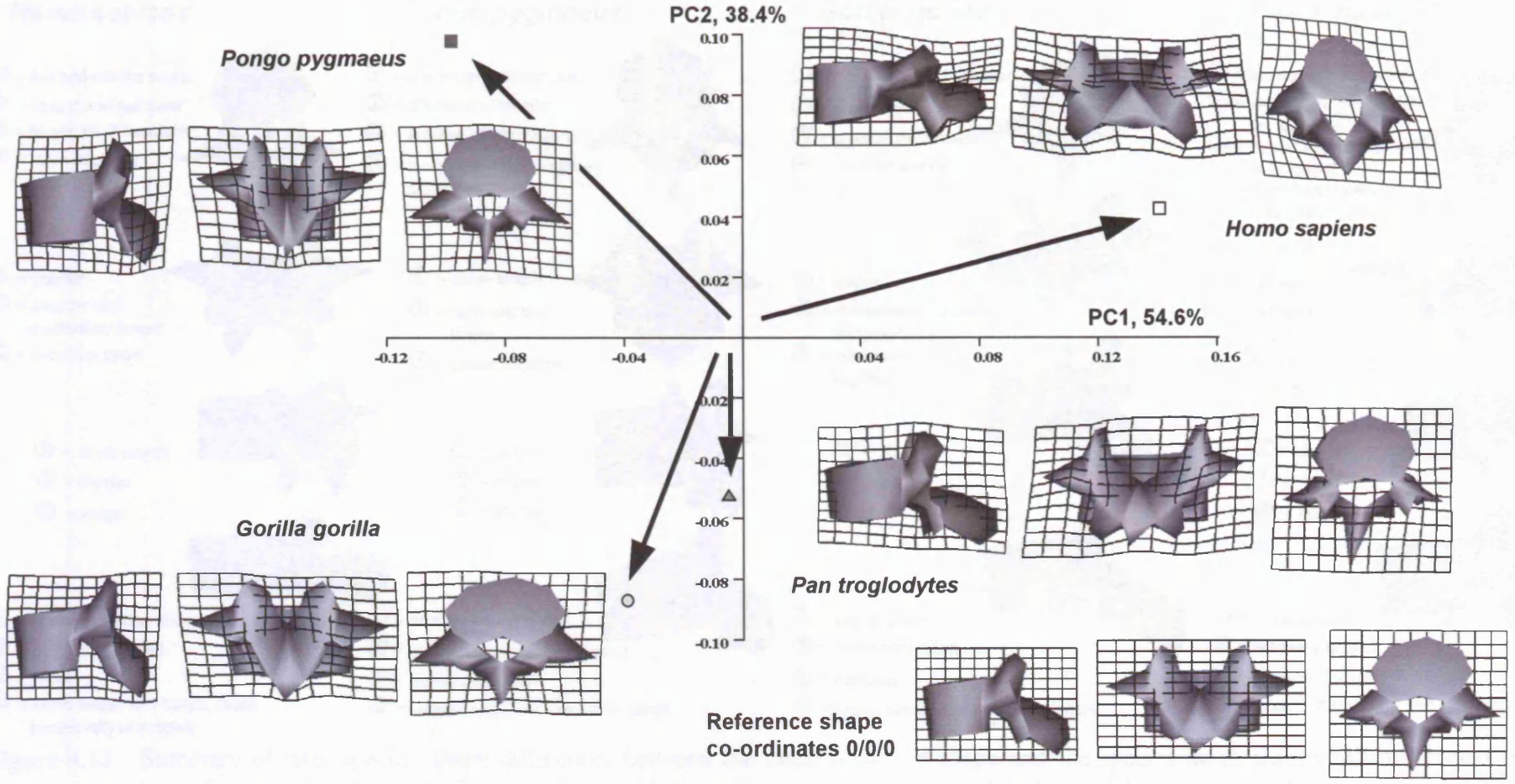


Figure 4.12 Scatter plot of PC1 vs. PC2, extracted from vertebral level means of modern taxa at comparison level 4. Reference shape = Mean hominoid shape calculated from all four taxa and located at coordinates 0/0/0); target shapes = taxon mean shapes of *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior and superior views (left to right). Grid positions indicate position of greatest grid distortion. □ = *Homo sapiens*, ○ = *Gorilla gorilla*, △ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

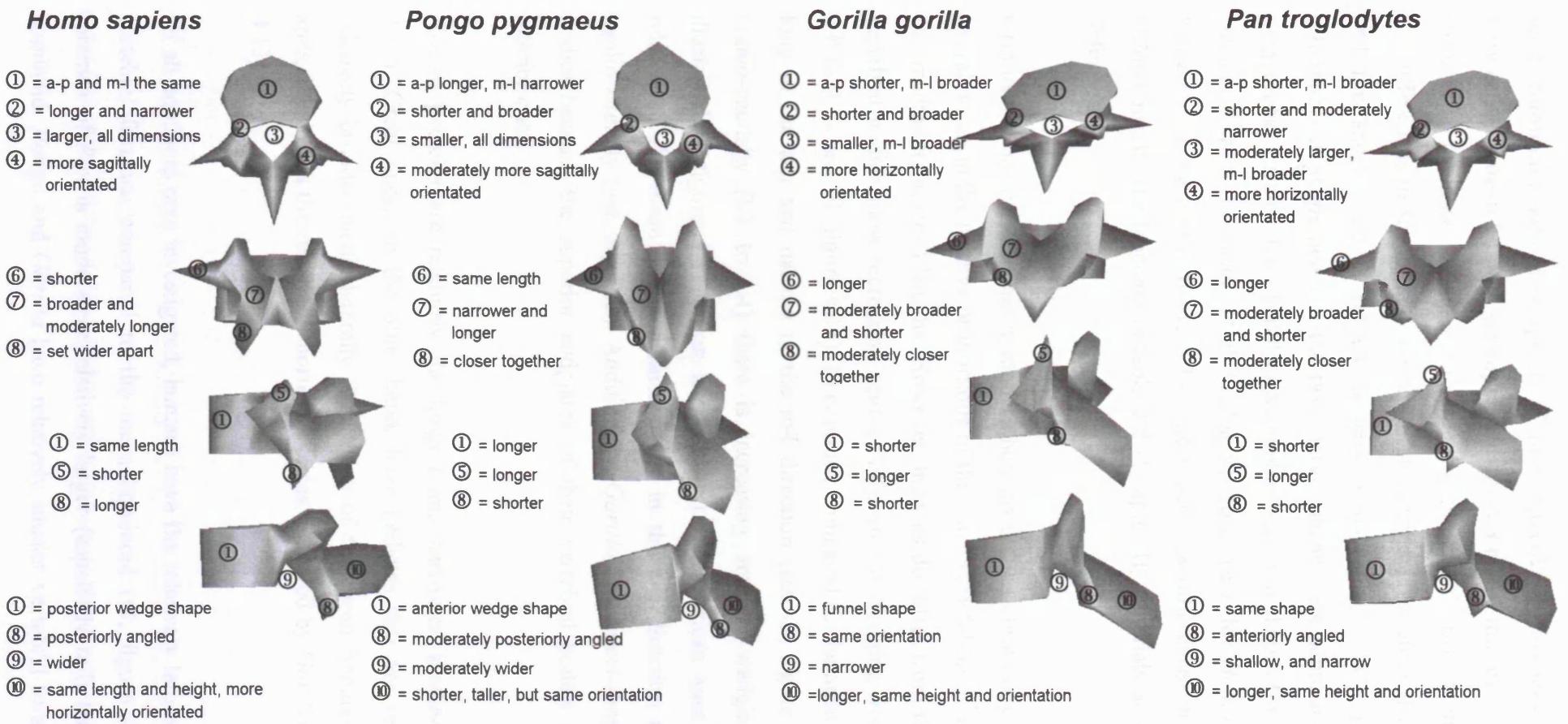


Figure 4.13 Summary of inter-specific shape differences between the mean hominoid shape and the species mean shapes. All differences in shape are referred to in relation to the mean hominoid shape (previous analyses, see fig. 4.7 to 4.11). All shape differences are relative to the mean hominoid vertebral shape and between the taxa. From top to bottom: superior, posterior, left postero-lateral, and left lateral views. ① = vertebral body ② = pedicles ③ = vertebral foramen ④ = superior articular joint facets ⑤ = superior articular processes ⑥ = costal processes ⑦ = vertebral arch ⑧ = inferior articular processes ⑨ = *Incisura vertebralis major* ⑩ = spinous process

4.6.5 Summary and description of inter-specific differences in vertebral shape between the mean hominoid shapes and species mean shapes

In order to facilitate reading and interpreting the grid distortions in figures 4.8 to 4.12, the differences in shape between the mean hominoid vertebral shape (reference shape) and the species means (target shapes), visualized by these grid distortions and differences in shape between the taxa (target shapes) are summarized in the following paragraphs. Further, the overall mean lumbar vertebral shapes for each taxon has been calculated from the means of all lumbar vertebrae (e.g. for *Homo sapiens* from L1 to L5) and is presented in figure 4.13. The order how differences in shape are presented follows mainly the labelling in table 2.8 (Chapter II, materials and methods, landmark definition).

Grid distortions indicate that in modern humans the vertebral body is very similar to the overall mean in the relative proportions of the cranio-caudal (c-c), antero-posterior (a-p) and medio-lateral (m-l) lengths. However, humans do differ from the mean in that their vertebral bodies show increasing degrees of posterior wedging from L1 to L5 (figures 3.8 to 4.12 and ①, figure 4.13). In contrast, compared to the mean, *Pongo* is relatively long in the a-p and narrow in the m-l direction (see ①, figure 4.13). Additionally, cranio-caudally (L1 to L4) there is increasing anterior wedging (particularly well illustrated in figure 4.12, mean last lumbars). The African apes on the other hand relative to the mean are moderately short in the a-p direction and relatively broad medio-laterally (see ①, 4.13). Additionally, *Gorilla* has funnel-shaped lumbar vertebral bodies because the superior endplates of their vertebral bodies are bigger than the inferior ones.

Human pedicles are relatively the longest and narrowest medio-laterally (②, figure 4.13). Great apes, on the other hand, have pedicles that are relatively shorter and relatively broader medio-laterally than those of the mean hominoid. Of all the great apes, *Pongo* has the relatively shortest pedicles, followed by *Gorilla* and *Pan* (②, figure 4.13).

Of all hominoid taxa investigated, humans have the relatively largest (in all dimensions) vertebral foramen compared to the mean hominoid (③, figure 4.13). The vertebral foramen of *Pan* is moderately relatively larger (especially m-l) than that of the mean hominoid. *Pongo* and *Gorilla* have relatively smaller vertebral foramina than the mean

hominoid however in *Pongo*. It is similarly shaped to that of the mean while in *Gorilla* it is more a-p flattened.

The superior articular facets of modern humans are more sagittally orientated than those of the mean hominoid (see ④, figure 4.13). Cranio-caudally, from L1 to L5, the degree of sagittal orientation increases. In *Pongo*, there is no difference in orientation of the superior articular facets observed in relation to the mean hominoid. However, the distance between the superior articular facets of *Pongo* is clearly relatively less than that of the mean hominoid. In both African ape taxa, the orientation of the superior articular facets is more horizontal than in the mean hominoid (see ④, figure 4.13).

Humans have relatively shorter superior and relatively longer inferior articular processes than the mean hominoid (see ⑤ and ⑧, figure 4.13). The latter are more posteriorly angled, which in results in a widely "gaping" human *Incisura vertebralis major* (⑨, figure 4.13). The degree of posterior angulation increases from the first to the last lumbar vertebra (see figures 4.8 to 4.12). All great apes, on the other hand, have relatively shorter inferior and relatively longer superior articular processes than the mean hominoid. In addition, only *Pongo* inferior articular processes are moderately posteriorly angled (see ⑧, figure 4.13). Nevertheless, compared to the mean hominoid, the *Pongo Incisura vertebralis major* is only moderately relatively wider, whereas it is relatively narrower in both African apes and most so in *Gorilla*. Of all the great apes, *Pongo* has the shortest inferior articular processes, followed by *Gorilla* and *Pan*. In humans, the tips of the inferior articular processes are set relatively wider apart than those of the mean hominoid. The relative distance between the tips of the inferior articular processes is relatively narrower than that of the mean hominoid. The relative distance between the tips of the inferior articular processes is also the shortest in *Pongo* in comparison to the mean hominoid and the other great ape taxa. The same relative distance in African apes is either similar to that of the mean hominoid (*Pan*) or moderately shorter (*Gorilla*).

The costal processes of modern humans are relatively shorter than those of the mean hominoid (⑥, figure 4.13). In *Pongo*, they are of approximately the same relative length as in the mean hominoid. In contrast, both African ape taxa have relatively longer costal processes than the mean hominoid. *Pan* surpasses *Gorilla* in relative costal process length.

The vertebral arches of *Homo sapiens* are relatively broader than those of the mean hominoid and become increasingly more so from comparison level 1 to 4 (see figures 4.8 to 4.12). They also are moderately relatively longer than in the mean hominoid yet their length decreases from L1 to L5. *Pongo* has the relatively longest and narrowest vertebral arches (⑦, figure 4.13). African apes have moderately broader and moderately shorter vertebral arches than the mean hominoid. *Pan* surpasses *Gorilla* in relative width as well as length of the vertebral arch.

The spinous process of modern humans is relatively shorter, cranio-caudally it is moderately relatively short, and its orientation is more horizontal than in the mean. *Pongo* has the relatively shortest and tallest (cranio-caudal direction) spinous processes (see ⑩, figure 4.13). However, they are more similar to the mean hominoid. The same is to be said of the orientation of the spinous processes of the African ape taxa. However, in the latter, the spinous process is relatively longer whereas its cranio-caudal dimension is either equal (*Pan*) or moderately relatively shorter (*Gorilla*). *Pan* surpasses *Gorilla* in relative spinous process length.

4.6.6 Analysis 5, assessing distances between species mean shapes at each comparison level with the help of UPGMA

To summarize and facilitate visualization of the high dimensional space of the analyses of species mean vertebral shapes, UPGMA phenograms were produced. These reduce the high dimensional space in which the species means are represented to a two-dimensional dendrogram. From the Procrustes cord distance matrices presented in table 4.6, matrix correlation coefficients were calculated at each comparison level and are found to give consistently high co-phenetic correlations (>0.89, see table 4.7) i.e. they well represent the multidimensional relationships in form in the two-dimensional trees. Figure 4.14 presents the UPGMA phenograms produced for each comparison level and table 4.7 summarizes the matrix correlation coefficients.

Level 1 (solution 1)	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*
Pan troglodytes	0.294241		
Gorilla gorilla	0.235996	0.116299	
Pongo pygmaeus	0.199649	0.234855	0.214534

Level 1 (solution 2)	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*
Pan troglodytes	0.272182		
Gorilla gorilla	0.222445	0.116300	
Pongo pygmaeus	0.211579	0.234860	0.214535

Level 2	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*
Pan troglodytes	0.252108		
Gorilla gorilla	0.208957	0.133232	
Pongo pygmaeus	0.220350	0.252028	0.218620

Level 3	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*
Pan troglodytes	0.244169		
Gorilla gorilla	0.192669	0.121244	
Pongo pygmaeus	0.198397	0.228333	0.195471

Level 4	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*
Pan troglodytes	0.223033		
Gorilla gorilla	0.183805	0.099436	
Pongo pygmaeus	0.245072	0.197328	0.184514

Table 4.6 Procrustes cord distance matrices calculated at all comparison levels and for all hominoid taxa (*Homo sapiens, Gorilla gorilla, Pan troglodytes*, and *Pongo pygmaeus*)

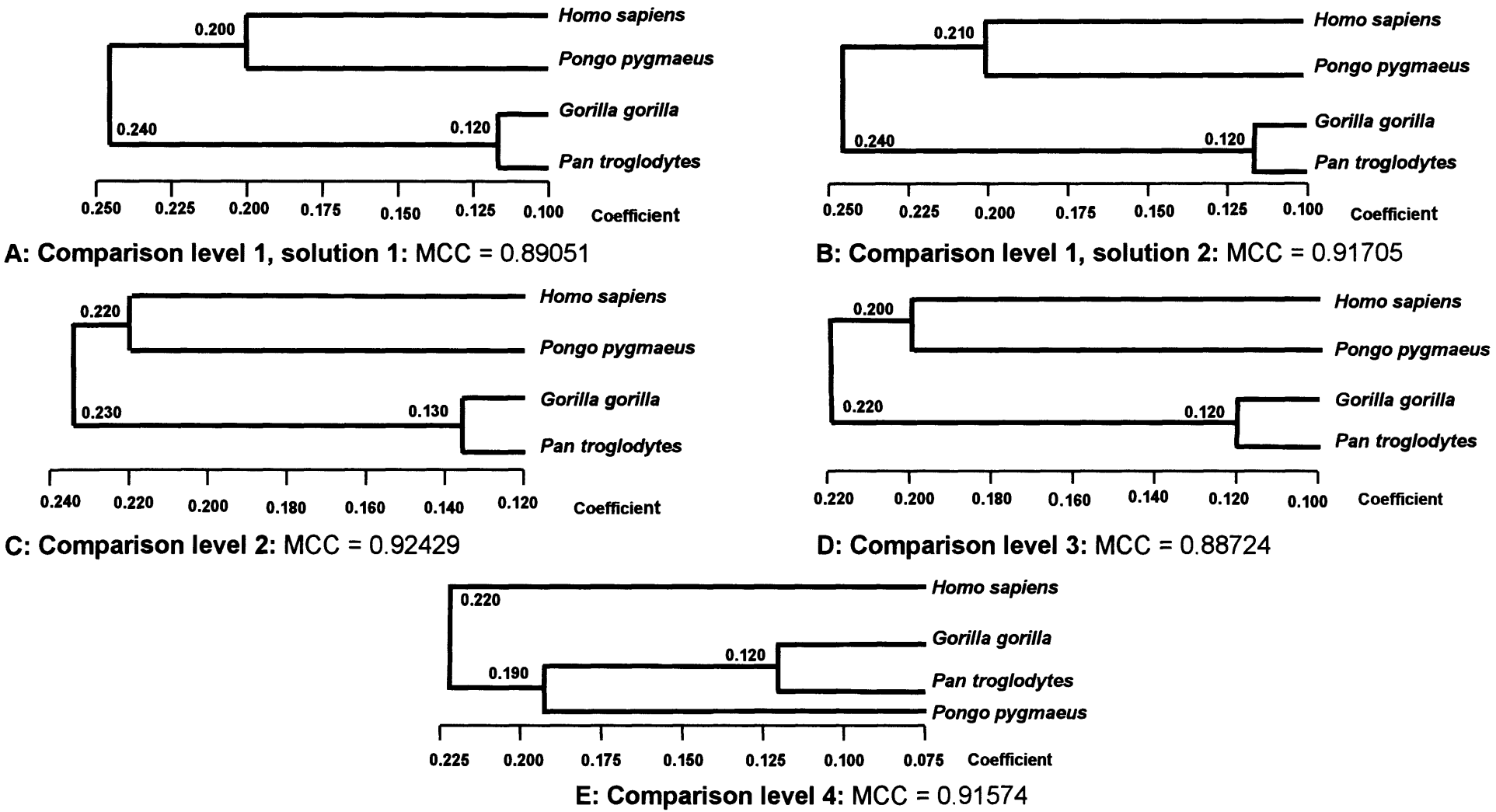


Figure 4.14 UPGMA phenograms constructed using Procrustes distances between mean vertebral shapes of all modern taxa. **(A)** to **(E)** Vertebral comparison levels 1, solution 1 to level 4. MCC = Matrix correlation coefficient (see table 4.6)

The results from the UPGMA analysis corroborate the results from the analysis of mean lumbar vertebrae (analysis 4 and 5). Thus, the UPGMA phenograms suggest more similarity between the mean vertebral shapes of *Homo sapiens* and *Pongo* than between *Homo sapiens* and the African apes. Again, the two African ape taxa are closest to each other. The exception from this is the last lumbar vertebra (see figure 4.14). The last lumbar vertebra of modern humans is the most different in shape from all other hominoids in the study hence at this comparison level, *Pongo* clusters first with the African apes.

Level	Figure	Cophenetic correlations
Comparison level 1, solution 1	4.15A	0.89051
Comparison level 1, solution 2	4.15B	0.91705
Comparison level 2	4.15C	0.92429
Comparison level 3	4.15D	0.88724
Comparison level 4	4.15E	0.91574
Mean shapes all taxa	Not shown	0.89100

Table 4.7 Cophenetic correlations for UPGMA phenograms at each vertebral comparison level

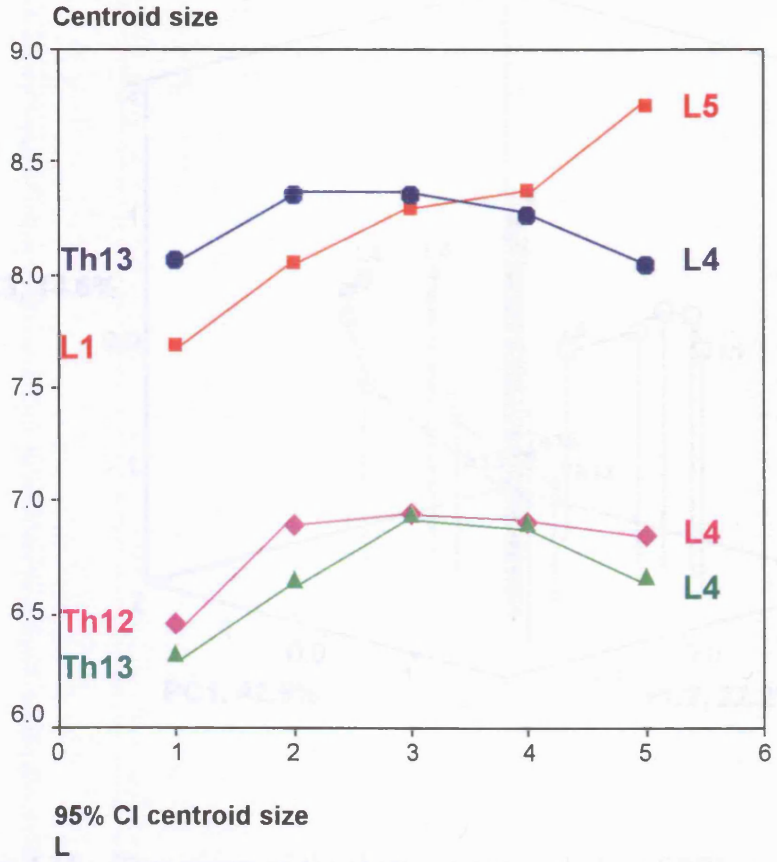
4.6.7 Analysis 6, comparison of adult patterns of inter-segmental size and shape variation along the lumbar spine

Patterns of vertebral size variation along the lumbar spine of each taxon are examined by plotting mean vertebral centroid size against vertebral level for each taxon. In the case of modern humans, this comprises lumbars 1 to 5 whereas in the case of the great apes, the last thoracic vertebra is included to make up equal numbers of vertebrae between humans and apes. Equal numbers of vertebrae produce patterns of same length which are easier to interpret and visualization is better. The plot is presented in figure 4.15A. In addition, figure 4.15B presents a box plot of the 95% confidence interval for the patterns of vertebral size variation patterns. Neighbouring vertebrae are connected with lines to facilitate visualization of patterns of metameric changes in vertebral size along the spine. Figure 4.15 shows that the pattern in humans differs from those of all great ape taxa. In modern humans, size steadily increases from L1 to L4. Between L4 and L5, the change in size is considerably larger than between other neighbouring vertebrae. In contrast, all great ape taxa show similar patterns which differ from the modern human one. Vertebral size increases from Th13 to the first (*Pongo*) or second

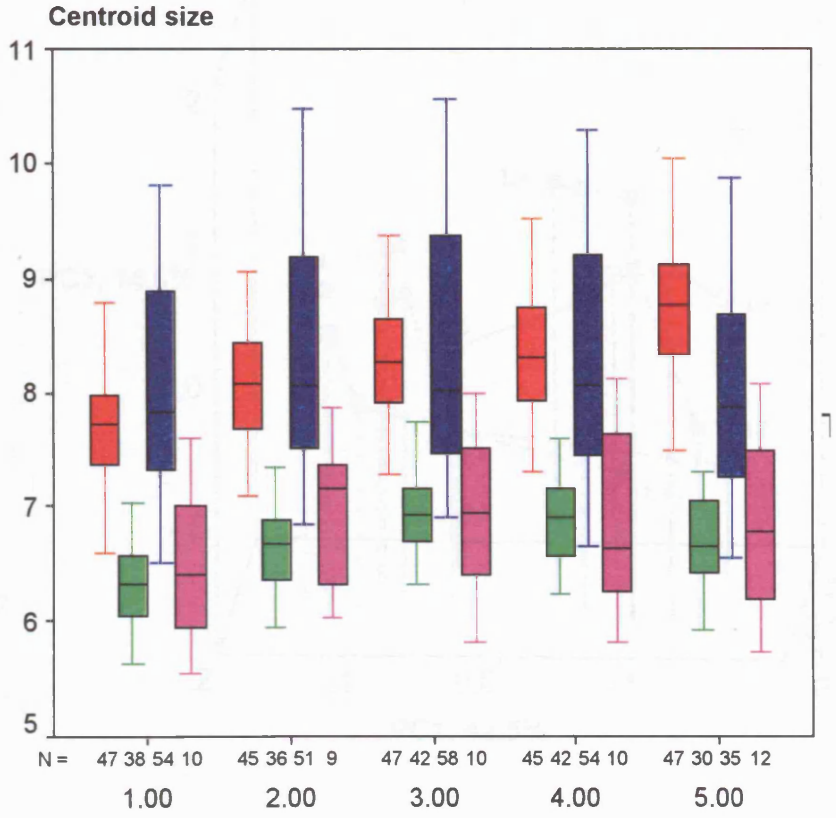
(African apes) lumbar vertebra and then decreases again towards L4. Both African ape taxa show more marked size decrease from L2 to L4 than *Pongo*. Nevertheless, the pattern of size increase and decrease is similar in all great apes.

GPA/PCA of the mean vertebral shapes of all lumbar vertebrae of all taxa was carried out to investigate, describe and visualize the patterns of inter-segmental (metameric) shape variation. The patterns of metameric variation in shape along the lumbar spine are visualized and presented in figures 4.16. Consecutive lumbar vertebrae of each hominoid species in the study are connected with lines. This facilitates the identification of each taxon in the shape space and makes it possible to trace and compare the patterns of metameric shape variation along the column in and between each taxon. Since the great apes only have four lumbar vertebrae, their last thoracic vertebrae have been included into the analysis so that the total number of vertebrae is the same (five) for humans and apes. However, analyses in which the last thoracic vertebrae were omitted in the apes did not significantly change the distribution of specimens on PCs1 and 2 for L1 to L4, therefore the impression from the PCA plots of the differences in patterns of metameric shape variation along the column is a good reflection of the scatters of vertebral means in the shape space. In appraising these plots the homology issue should however be borne in mind.

Figure 4.16 presents different views of a three-dimensional scatter plot (PC1 vs. PC2 vs. PC3). These PCs collectively summarize 80% of the total shape variance. The plot indicates that patterns of inter-segmental shape variation are different in *Homo sapiens*, *Pongo* and the African apes. *Homo sapiens* differs greatly from all great apes. The patterns of African apes, on the other hand, are very similar to each other. *Pongo* shows a different pattern from both, modern humans and African great apes.



A: Patterns of vertebral size variation (mean vertebral shapes)



B: 95% confidence intervals for each vertebra (full samples)

Figure 4.15 Patterns of vertebral size variation along the lumbar spine: adult specimens only. Note the differences in patterns between humans and all other hominoid taxa. **(A).** 95% confidence interval, vertebral size at each vertebral level; **(B)** L1, Th12, Th13 and L5, L4 respectively are labelled. Full sample n = 722; ■, ■= *Homo sapiens*, ●, ■ = *Gorilla gorilla*, ▲, ■ = *Pan troglodytes*, ♦, ■ = *Pongo pygmaeus*

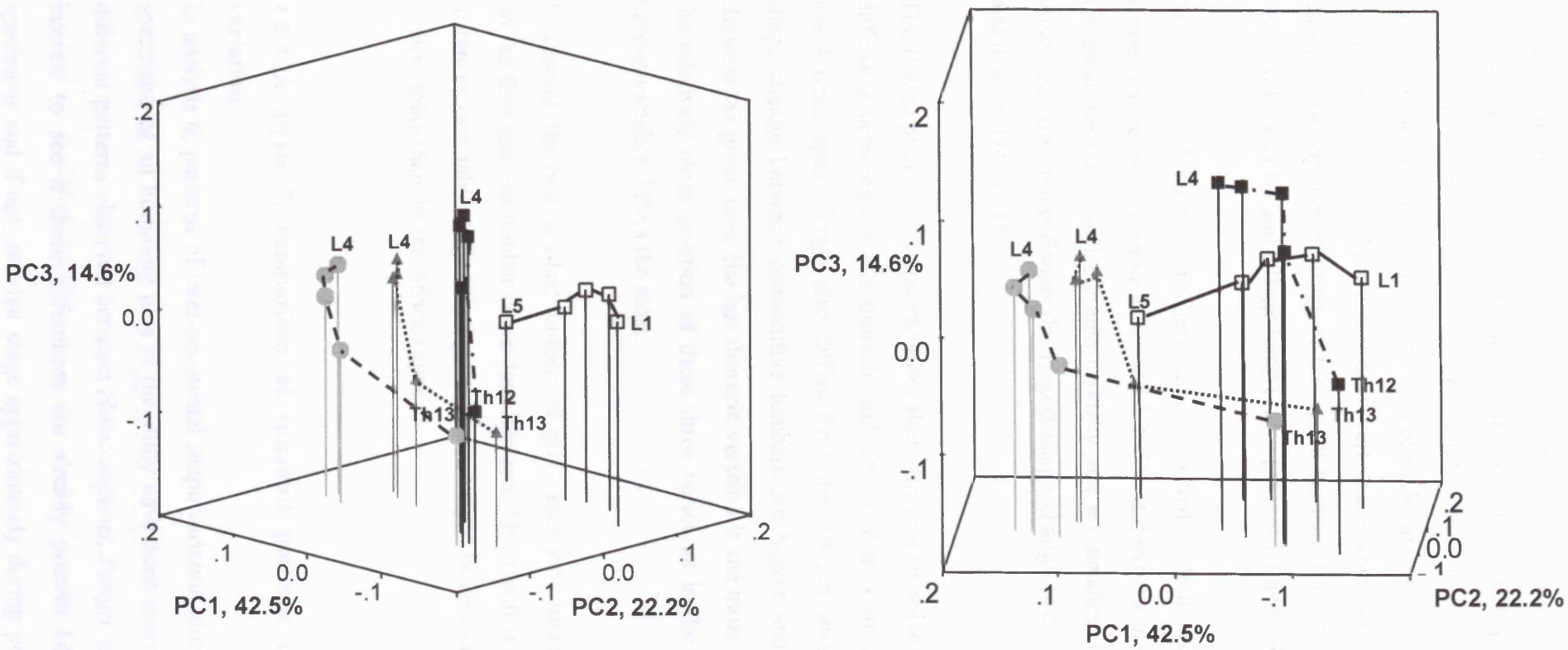


Figure 4.16 Two views of the three-dimensional plot of PC1 vs. PC2, vs. PC3, adult mean lumbar vertebral shapes, all modern. L1, Th12, Th13 and L5, L4 are labelled to indicate the position of consecutive vertebrae which are connected by lines in each taxon. Spikes indicate relative positions of the consecutive vertebrae of each taxon in the plot □ = *Homo sapiens*, ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

Particular interest is focused on the shape of the curve connecting mean vertebrae because that shape reflects the nature and magnitude of shape changes along the lumbar spine of the different taxa. Inter-specific differences in patterns of metameric variation consist of the differences in the location of each curve in the space of the first three PCs (indicating differences between taxa in vertebral shape) and in the magnitudes of shape change between neighbouring vertebrae: In humans, the largest "jump" in shape occurs between L4 and L5 and a large jump is also present L3 and L4.

African apes differ from modern humans in that – along the lumbar spine, the largest shape change occurs between L1 and L2. The differences in shape between consecutive vertebrae become smaller cranio-caudally and are smallest between L3 and L4. In all great apes (including *Pongo* the largest shape change occurs between the last thoracic and first lumbar vertebra.

The *Pongo* pattern of shape variation along the lumbar spine differs yet again in that the difference between the last thoracic and first lumbar is smaller than those observed in the African apes. *Pongo* also differs from the African apes in that the differences in shape change between consecutive lumbars are bigger and more even in magnitude. Between all great apes, the last thoracic vertebra is the most similar. This is indicated by the relatively close position of these three vertebrae in the plots. In contrast, the last lumbar vertebra differs the most.

In general, the first and last lumbars of great apes look more similar to each other than do the first and last lumbar of modern humans. This result is corroborated by Procrustes distances (see table 4.6). Of all great apes, *Pongo* shows more shape variation along its lumbar spine than do the African apes.

4.6.8 Analysis 7, comparison of subadult patterns of inter-segmental shape variation

In analysis 6, patterns of inter-segmental shape variation along the lumbar spine of adult specimens of all hominoid taxa in the study have been examined. Since there are three different patterns observed between *Homo sapiens*, *Pongo*, and the African apes, it is of interest to see if these differences are already present between the most immature specimens and if not, at what stage approximately during postnatal ontogeny they start

to differ from each other. Analysis 7 employs the same techniques as analysis 6, namely GPA/PCA on all mean lumbar vertebral shapes of all hominoid taxa in the study, PC plots in two and three dimensions, lines connecting consecutive vertebrae. However, the two samples investigated here consist of; younger (infant) specimens and older (juvenile) specimens.

The results are yet again presented in a three-dimensional plot of PCs 1, 2, and 3. In both analyses (infant and juvenile sample) PCs 1 and 2 summarize approximately 74.6% (infant) and 85.5% (juvenile) of the total shape variance The study reveals that differences in inter-segmental shape variation patterns between the taxa are established in early postnatal ontogeny, thus are highly likely already present prenatally (see figures 4.17 and 4.18). However, there are fewer differences in the patterns observed between infant specimens of all great ape taxa (see figure 4.17) than between the adult specimens of the same taxa. The differences in inter-segmental patterns of shape change between humans and all great apes, on the other hand, are already visible in the infant sample although in the case of humans this result is highly tentative given that only a single individual is included (see figure 4.17). Interestingly, the pattern of inter-segmental shape variation in infant *Pongo* resembles that of the infant African apes far more than the adult *Pongo* pattern resembles the adult African ape pattern. However, comparing the juvenile *Pongo* pattern with the juvenile African ape pattern (figure 4.18), the differences observed between the adult *Pongo* and adult African ape pattern emerge clearly.

In both the analyses of infants and that of juveniles, African ape inter-segmental patterns of shape variation are very similar to each other. The difference in shape between the last thoracic and the first lumbar becomes more pronounced from infant to adult patterns at all ages. The same obtains for the differences between L4 and L5 in modern humans.

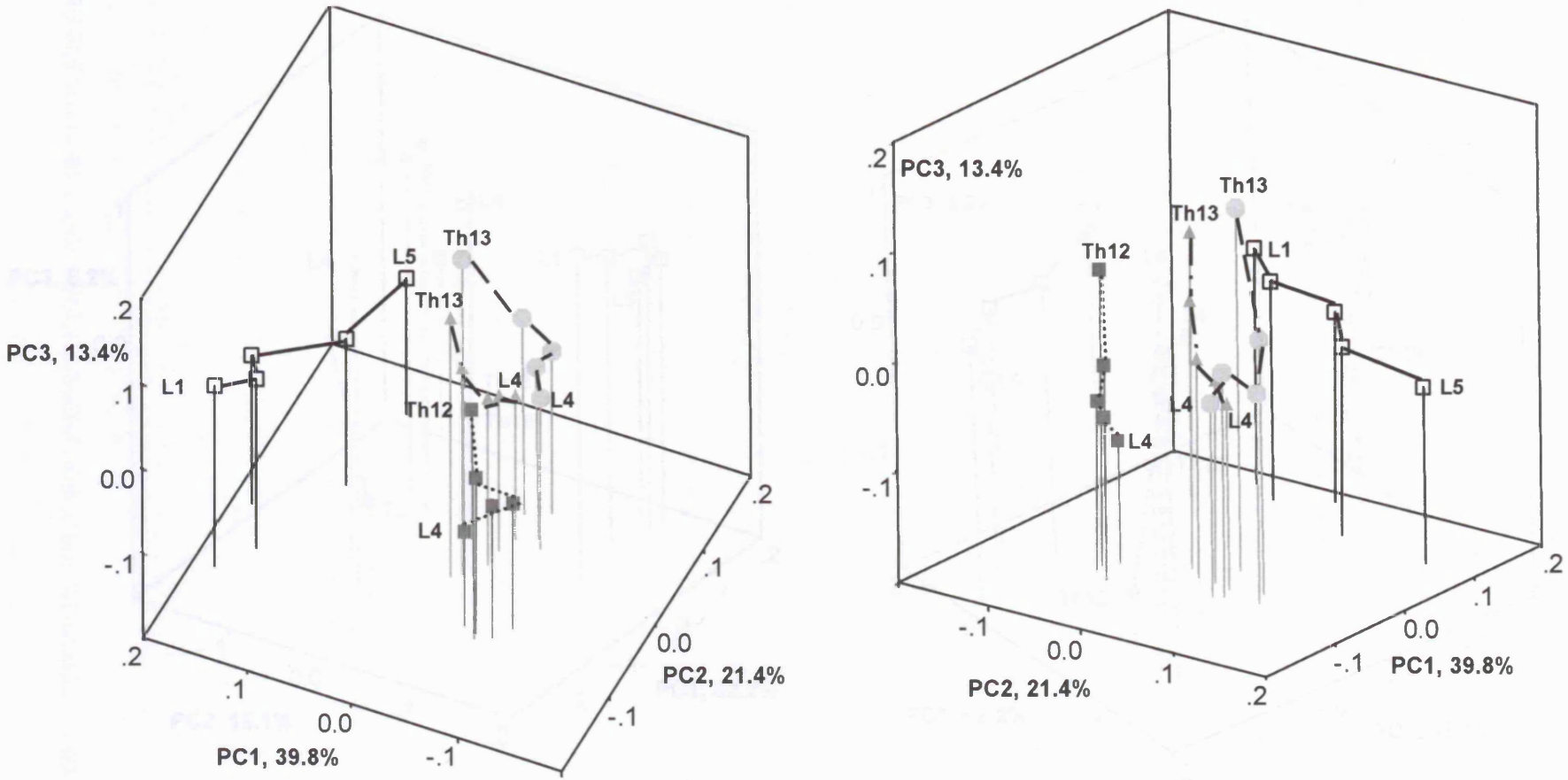


Figure 4.17 Two views of the scatter plot PC1 vs. PC2, vs. PC3, mean infant lumbar vertebral shapes, all modern taxa. L1, Th12, Th13 and L5, L4 respectively are labelled. Spikes indicate relative position of the consecutive vertebrae of each taxon within the plot □ = *Homo sapiens*, ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

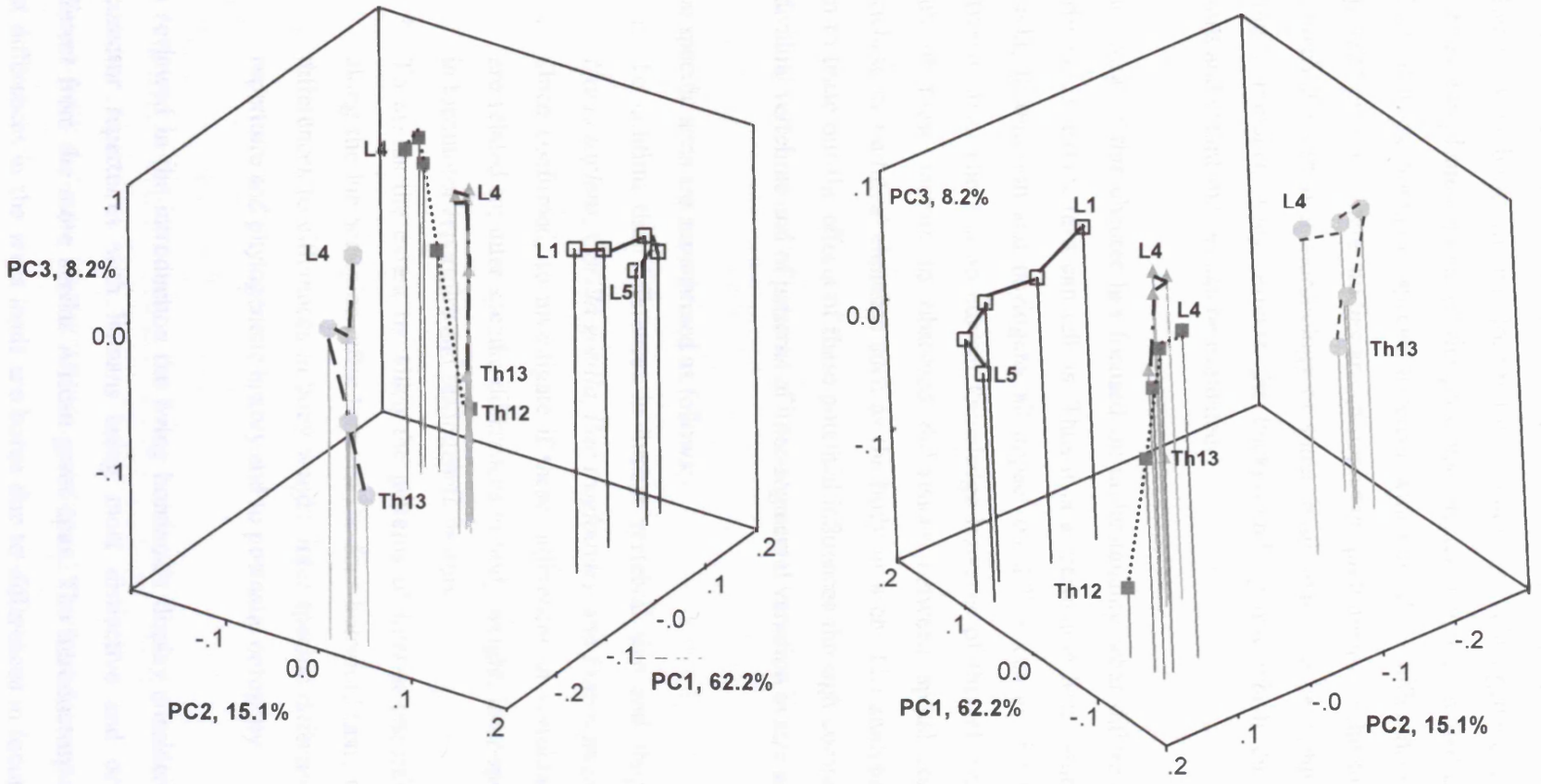


Figure 4.18 Two views of the scatter plot PC1 vs. PC2, vs. PC3, mean juvenile lumbar vertebral shapes, all modern taxa. L1, Th12, Th13 and L5, L4 respectively are labelled. Spikes indicate relative position of the consecutive vertebrae of each taxon within the plot □ = *Homo sapiens*, ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*

4.7 Discussion

This study has examined differences in vertebral morphology (size and shape) between hominoid taxa. The aim has been to examine the extent to which such differences reflect differences in body weight, locomotor function and phylogenetic relationships. The findings complement those of the previous chapter which examined differences within adults of living hominoid species together with how these differences arise during the postnatal period. These studies are an important preliminary to the subsequent chapter in which the vertebral morphology of some fossil taxa is to be compared with that of living hominoids. They provide the background against which differences between fossils and extant species can be evaluated.

The work of this chapter has focused on understanding what differences between the vertebrae of extant taxa can tell us. Thus it is a reasonable first assumption that body weight, locomotion and phylogeny all impact on differences in vertebral morphology between taxa. There is no current knowledge however of the relative contribution of each of these factors to observed differences between spinal regions, individual vertebrae or vertebral elements such as the body or arch. The analyses of this chapter aim to tease out the effects of these potential influences through comparative studies of individual vertebrae and of patterns of inter-segmental variation in size and shape.

The specific aims are summarized as follows:

1. To confirm that differences in lumbar vertebral size and shape exist between *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*
2. Once confirmed, to investigate if these differences in vertebral size and shape are related to; inter-specific differences in body weight, inter-specific differences in locomotor repertoire and phylogenetic history
3. To assess the extent to which the patterns of inter-segmental shape variation along the lumbar spine differ between the four hominoid taxa, relating any such differences to differences in body weight, inter-specific differences in locomotor repertoire and phylogenetic history and to postnatal ontogeny

As reviewed in the introduction the living hominoids display considerable diversity of locomotor repertoires with humans being most distinctive and orang-utans being different from the more similar African great apes. The introductory review indicated that differences in the ways loads are borne due to differences in locomotion are likely

to impact on the morphology of those vertebral elements that are responsible for the articulation and ranges of motion of vertebrae and regions of the vertebral columns and which provide attachment for the muscles controlling vertebral motion. Thus it is expected that locomotor differences impact mostly on the zygapophyseal joints and the processes. Additionally since locomotion affects the ways in which body weight is transmitted to the substrate (ground or tree) it is likely that differences in locomotion as well as differences in body mass will have an impact on those weight bearing structures of the spine, which include, anteriorly the bodies and posteriorly the arches and their articulating structures. Further the vertebrae arise through the operation of inherited genes that pattern and influence the subsequent changes in vertebral size and shape during development. Thus it is reasonable to expect that differences in phylogeny will also have an impact on vertebral morphology.

The analyses of this study have been driven by a series of hypotheses that arose from the considerations of locomotor function, body weight variation and phylogeny raised in the introduction. These hypotheses are organised as six groups. The first four of these deal with differences between vertebral levels, taken one at a time. The first addresses inter-specific differences in vertebral size and shape, the second addresses relationships between vertebral size and shape and differences in body weight, the third addresses the impact of locomotion of vertebral size and shape, and the fourth phylogeny. The fifth and sixth hypotheses deal with differences between taxa in the ways in which the last five presacral vertebrae show inter-segmental patterns of size and shape variation. This discussion is organised according to the study aims:

4.7.1 Do differences in lumbar vertebral size and shape exist between *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*

Before one can examine the relationship between differences in vertebral size and shape and factors such as differences in body weight, locomotor repertoires, and phylogeny, the presence of differences in vertebral size and shape have to be confirmed. Thus, hypotheses 1.1 (differences in vertebral size) and 1.2 (differences in vertebral shape) were formulated. They simply address the questions of presence or absence of inter-specific differences in vertebral size and shape.

In analysis 1, addressing hypothesis 1.1, differences in vertebral centroid sizes were calculated between pairs of taxa (e.g. *Homo sapiens* - *Gorilla, Homo sapiens* – *Pan*, etc) at each comparison level. The significance of differences in centroid size between each possible pair of taxa was tested with independent t-tests.

Analyses 2, 3, and 4, which address hypothesis 1.2, investigated the significance of differences in vertebral shape between pairs of taxa (analysis 2), the scatters of specimens (analysis 3), and species means (analysis 4) in GPA/PCA analyses.

Analysis 2 assessed the significance of differences in shape between pairs of taxa by calculating the Procrustes mean distances between vertebral shapes of pairs of taxa at each vertebral comparison level. The significance of shape differences between two taxa was tested with permutation tests. Analysis 3 used GPA/PCA to examine the scatters of all the hominoid specimens to observe the degrees of overlap or differentiation between taxa. PCs which summarized differences in shape between species were identified with step-wise discriminant analysis and this analysis confirmed that differences were sufficient to identify vertebrae to taxa. Analysis 4 explored the relationships between species mean shapes of each taxon using GPA/PCA.

The results from analysis 1 show vertebral sizes differ significantly between all hominoid taxa. However, exceptions are observed between *Gorilla* and *Homo* and *Pan* and *Pongo* where differences in vertebral size did not meet significance levels. *Gorilla* and *Homo sapiens* have the largest lumbar vertebrae, followed by *Gorilla* females and *Pongo* males, *Pan* males and females, and *Pongo* females. These results lead to the falsification of hypothesis 1.1 because there are significant differences in vertebral centroid size observed between the hominoid taxa (with two exceptions). They (including the exceptions) agree well with those reported by other authors. Schultz finds that humans and *Gorilla* have the largest lumbar vertebrae followed by *Pongo* and *Pan* (Schultz, 1931; Schultz, 1950a; Schultz, 1953; Schultz, 1961; Schultz, 1969a; Schultz and Straus, 1945). The exceptionally large single lumbar vertebrae of modern humans (in comparison to great apes of comparative body weight) have previously been interpreted as an adaptation to resist high amounts of compressive forces and to support of body weight in orthograde trunk posture in relation to bipedal gait (Rose, 1975; Sanders, 1998; Schultz, 1953; Shapiro, 1993a; Shapiro, 1993b).

Results from analyses 2, 3, and 4 show that vertebral shape differs significantly between all hominoid taxa. The vertebral shape of *Homo sapiens* is most different from all great ape taxa. That of *Pongo* differs clearly from both African ape taxa, whereas *Gorilla* and *Pan* have the smallest differences in shape between all taxa. These results falsify hypothesis 1.2 because they show significant differences in vertebral shape between all hominoid taxa. Differences in vertebral shape between humans and great apes have been extensively reported in previous studies by (Benade, 1990; Odgers, 1933; Sanders, 1998; Shapiro, 1990; Shapiro, 1993a; Slijper, 1946; Sonntag, 1924; Ward, 1997). Differences in vertebral shape observed between modern humans and great apes are interpreted as adaptations to differences in weight transmission and loading patterns of the vertebrae and differences in how muscles attach to the vertebral processes.

Summary

In summary, it can be concluded that lumbar vertebral size and shape differ significantly between hominoid taxa. Results from analyses 1 and 2 confirm the presence of significant differences in vertebral size and shape between the hominoid taxa. In the following sections, we discuss the results from our investigation of the relationships between differences in vertebral size and shape and differences in body weight, locomotion, and phylogeny.

4.7.2 Do differences in vertebral size and shape relate to inter-specific differences in body weight?

To investigate how differences in vertebral size and shape are related to inter-specific differences in body weight, hypotheses 2.1 (size) and 2.2 (shape) have been formulated.

Hypothesis 2.1 is tested by looking for a relationship between inter-specific differences in vertebral size and differences in body weight. Hypothesis 2.2 was formulated to assess the presence or absence of a relationship between inter-specific differences in vertebral shape and differences in body weight.

To address hypothesis 2.1, body weights and centroid sizes were compared between taxa taking into account sexual dimorphism in these comparisons (see 4.6.1). Apes of similar weight possess vertebrae of similar centroid size, while differences in weight are reflected in differences in centroid sizes. Thus there is a relationship between body

weight and centroid size among apes. Humans are unusual in possessing relatively large lumbar vertebrae for their body weight. Thus for apes hypothesis 2.21 is falsified, but in humans it appears that functional specialisations (probably for running rather than walking - see Chapter V) break this relationship.

Hypothesis 2.2 was addressed by Procrustes distances between mean lumbar vertebral shapes (calculated between Levels 1 and 4 in each taxon; analysis 2) in relation to differences in body weights. No relationship is apparent.

Summary

To summarize, the results lead to the falsification of hypothesis 2.1 although human locomotor adaptations skew the picture. Hypothesis 2.2 on the other hand cannot be falsified (no relationship is observed between differences in body weight and vertebral shape). It can be concluded that vertebral size differences have a marked relationship with differences in body weight between great ape taxa. However, the inclusion of humans obscures this. This is because human weight transmission mechanisms through the lumbar spine differ considerably from all other great apes. In contrast differences in body weight are not related to differences in vertebral shape between hominoids. This leads to studies of the impact of locomotor repertoires and phylogeny on vertebral size and shape differences.

4.7.3 Do differences in vertebral size and shape relate to inter-specific differences in locomotor repertoire?

To investigate how differences in vertebral size and shape are related to inter-specific differences in locomotor repertoires, hypotheses 3.1 (vertebral size) and 3.2 (vertebral shape) were formulated.

Hypothesis 3.1 tests for the presence or absence of a significant relationship between inter-specific differences in vertebral size and differences in locomotor repertoires. Hypothesis 3.2 was formulated to assess the presence or absence of a relationship between inter-specific differences in vertebral shape and differences in locomotor repertoires.

To assess the relationship between differences in vertebral size and locomotor repertoires (hypothesis 3.1), differences in vertebral size between the taxa (calculated in analysis 1) are compared with differences in locomotor repertoires between the taxa.

Results from analysis 1 (inter-specific differences in vertebral centroid size), show that lumbar vertebrae of humans and *Gorilla* are of similar size, whereas those of *Pan* and *Pongo* are smaller. Differences in locomotor repertoires, however, set humans apart from all great apes. The locomotor repertoire of *Pongo* is different from both, humans and African apes. The latter show relatively similar locomotor patterns when compared to *Pongo* and *Homo*. In the case of great apes, there is no relationship observed between differences in vertebral size and differences in locomotor repertoires. This is in contrast to the significant relationship observed between body weight and vertebral size (hypothesis 2.1.). However, in modern humans, the locomotor repertoire is most different from all other taxa yet its mean vertebral body size is very similar to that of *Gorilla*. This is explained by the findings of the tests of hypothesis 2.1 in which it was shown that the vertebral size of modern humans is larger than would be expected because of adaptations to bipedalism. In general then, differences in mean vertebral size between taxa are not a good reflection of locomotor repertoires unless body weight is also taken into account.

To address hypothesis 3.2 (vertebral shape in relation to locomotion), inter-specific differences in vertebral shape (explored in analyses 2, 3, and 4) are compared with differences in locomotor repertoires. Results from analyses 2, 3, and 4 (analysis of Procrustes distances, GPA/PCA analysis of full adult samples and of species mean shapes) indicate that modern humans are most different in vertebral shape from all other taxa, followed by *Pongo*. The African apes show relatively similar vertebral shapes. In contrast to the study of size, above, these results strongly reflect differences in locomotor repertoires between the taxa: humans have the most distinct locomotor repertoire from all great apes, followed by *Pongo* whereas African apes are also relatively similar in their locomotor repertoires.

Inter-specific differences in vertebral shape and locomotor repertoires between humans and great apes

Differences in lumbar spine morphology between modern humans and great apes are related to differences in weight bearing mechanisms and to the mobility of the lumbar

spine. These are both related to differences between the habitual bipedal gait of modern humans and the quadrupedal locomotion of the great ape taxa: the habitual orthograde posture and bipedal gait of modern humans requires not only a robust lumbar spine that can bear large loads on a small supporting area but the lumbar spine (when compared to great apes) has to be highly flexible to act as a shock absorber and to balance the vertebral column permanently over the pelvis (see Chapter I, pp. 41-42).

Differences in weight transmission and vertebral shape between humans and great apes

Differences in vertebral shape between humans and apes which are related to differences in weight and transmission and loading patterns of the lumbar spine have previously been described in detail by Boszczyk et al. (2001), Farfan (1978), Martelli and Schmid (2003), Pal and Routal (1987), Rose (1975), Sanders (1994), Schultz (1950b, 1961), Schultz and Straus (1945), Shapiro (1993a), and Sljiper (1946).

Several workers have noted such differences in the vertebral body, the pedicles, the articular processes and the costal processes of the last lumbar vertebra (Adams and Hutton, 1983; Boszczyk et al., 2001; Davis, 1961; Gracovetsky, 1986; Kapandji, 1992; Pal and Routal, 1987; Shapiro, 1993a; Slijper, 1946). The results from analysis 4 (comparing species mean shapes) indicate that differences in vertebral shape between modern humans and all great apes observed in this study are very similar to those described by other authors. This includes especially the shape of the lumbar vertebral bodies and pedicles (Rose, 1975; Shapiro, 1993a). In the case of differences in pedicle shape, the results from this study somewhat disagree with those reported by Shapiro (1993a). This is mainly due to different approaches to the same vertebral element. Whereas Shapiro investigated interlandmark distances and ratios of pedicle length to pedicle width as a proxy of pedicle "shape" (Shapiro, 1993a), this study only accesses relative scaled dimensions. Thus, in the present analyses, humans consistently had relatively narrower and longer pedicles than the other great ape taxa. In relation to pedicle dimensions, humans also consistently had the relatively largest vertebral foramina. However, at the level of the last lumbar, results from the present study agree with those from Shapiro (1993a) in that humans have the relatively largest and shortest pedicles on that vertebra.

Some of the differences in shape observed in this study are rarely mentioned in previous studies and should be highlighted here again. Among these are the length of the inferior articular processes and the posterior angulation of the same processes in humans (when compared to great apes). Sanders (1998) briefly mentions the posterior angulation of the inferior articular processes. He postulates that it serves as an adaptation to the permanent human lumbar lordosis. Nevertheless, no comment is provided on whether this angulation is thought to be a pre-adaptation to the lumbar lordosis or whether it is considered a consequence resulting from the permanent lordotic posture of the human lumbar spine.

Differences in lumbar spine mobility and vertebral shape between humans and great apes

As seen previously, inter-specific differences in the morphology of some vertebral elements between humans and all great apes are highly likely related to differences in load transmission through the vertebral column during locomotion. Other vertebral elements are usually thought to vary with inter-specific differences in lumbar spine mobility (especially between two consecutive vertebrae) between humans and all great apes (Benade, 1990; Sanders, 1994; Shapiro, 1990; Shapiro, 1993a). Lumbar spine mobility partially depends on the architecture of vertebral elements (e.g. the vertebral processes and the shape of the articular facets) and partially on the ligaments and muscles acting on the vertebrae (the back and shoulder muscles with origin and insertion in the lumbar spine). Chapter I (pp. 83 onward), describes in detail how these difference in shape have been described by other authors and how they are interpreted. Briefly, results from the present study (especially from analysis 4, differences in shape between species means) are very similar to those from previous studies but there are a few additional features.

Costal processes vary in relative length (lateral projection) between humans and great apes (see figure 4.14). In general, their cranial and dorsal orientations are very similar to each other. This confirms results reported by Shapiro (1993a) and Sanders (1998). Differences in the length and orientation of spinous process between humans and great are not so easily interpreted without detailed information about origin and insertion of back muscles into these vertebral elements. In addition, differences in the length of the articular processes between humans and great apes are highly likely also related to differences in lumbar spine mobility (especially in sagittal flexion-extension).

Thick intervertebral discs set neighbouring vertebrae farther apart from each other. As a consequence, human vertebral arches and especially the inferior zygapophyseal processes are relatively longer compared to great apes to bridge the larger gap. The elongated inferior zygapophyseal processes, in combination with the large lumbar intervertebral discs, enhance the mobility of the lumbar spine in modern humans.

African great apes, in contrast, have remarkably short vertebral arches and inferior articular processes when compared to modern humans. This is probably due to the fact that great apes do not have very thick intervertebral discs when compared to modern humans. Although data are published on the height of great ape intervertebral discs, limited personal observations on a chimpanzee specimen housed in the animal collection of the anatomy department, UCL, indicate that great ape intervertebral discs are likely to be considerably thinner than those of modern humans. In that particular specimen they never exceeded 5 mm. Therefore, great ape articular processes and arches are relatively short.

Differences in locomotor repertoires and vertebral shape between African and Asian great apes

Differences in vertebral shape between the great ape taxa are smaller than those observed between humans and great apes. To date, there is not a great deal of data published on vertebral shape differences. In general though, differences in vertebral size and shape between great apes are reported in studies where the great ape taxa serve as comparison taxa to modern humans. Thus, Sanders (1994) reports a somewhat different pattern of pedicle origin of costal processes in *Pongo* when compared to African apes. Shapiro (1993a) mentions some differences in pedicle shape between *Gorilla* and *Pongo*.

Although the differences in weight transmission seem to be small between all great ape taxa, there are substantial differences observed between the locomotor repertoires of great apes (especially between African and Asian apes) (Hunt, 1991b; Isler, 2005). The falsification of hypothesis 3.2 indicates that inter-specific differences in vertebral shape between the great apes are related to differences in locomotor repertoires between the African and Asian great apes.

Differences in loading patterns during locomotion between African and Asian great apes might serve as an explanation as to why *Pongo* has relatively long and narrow and anteriorly wedge shaped lumbar vertebral bodies when compared to both African apes. The earlier summary of inter-specific differences in locomotor repertoires between Asian and African apes indicates that the latter have lumbar spine loading patterns which are characterized by peak force impacts during fast terrestrial locomotion. *Pongo* is predominantly an arboreal species and its mode of propulsion is greatly forelimb dominated (Ashton et al., 1965a; Hunt, 1991b; Martin, 1990). *Pongo* is highly likely the most effectively adapted great ape taxa to tension-bearing in the upper limb due to its predominantly arboreal locomotor repertoire (Oxnard, 1983). In addition, Schultz (1953) notes that *Pongo*, in contrast to African apes, does not use its hindlimbs in the same way in locomotion. Thus, the *Pongo* vertebral column is exposed to a high proportion of tensile forces whereas the compressive load on their spine is probably somewhat reduced. Under axial loads, long narrow lumbar vertebral bodies are subject to higher bending stresses (Taylor, 1984). In light of their locomotor repertoire (large proportions of hanging-climbing and scrambling), which highly likely subject the *Pongo* spine to greater amounts of tensile stress than compressive stress, this could explain the particular shape of their lumbar vertebral bodies. Since the *Pongo* locomotor repertoire lacks high speed (galloping) and high force impact locomotor patterns (jumping) (Cant, 1987a; Hunt, 1991b; MacKinnon, 1974), this might also influence the degree of compressive strain to which the *Pongo* lumbar spine is subject.

Interestingly, the larger "gaps" between two consecutive *Pongo* lumbar vertebral bodies seem to be bridged by cranio-caudally elongated vertebral arches. *Pongo* has the second longest vertebral arches after modern humans. Since it is their vertebral arch that is elongated and not their articular processes, the mobility of their lumbar spine is nevertheless restricted and not enhanced as seen in modern humans.

Differences in locomotor repertoires and vertebral shape between African and Asian great apes

Results from analyses 3 and 4 (exploring differences in vertebral shape between large samples of each taxon as well as between species mean shapes) indicate that there are significant, albeit small differences in vertebral shape observed between the two African ape taxa. Since these shape differences are located mainly on the vertebral body, the length of the articular processes, and relative size and orientation of the spinous process,

one concludes that the substantial differences in body weight between the two taxa are at least in part related to these differences (spinous process orientation being subject to the vectors of loadings).

Summary

The partial falsification of hypothesis 3.1 (vertebral size in relation to locomotion) shows that differences in vertebral size between the taxa reflect differences in locomotor repertoires between humans and all great apes. Differences in vertebral shape on the other hand (falsification of hypothesis 3.2), reflect differences in locomotor repertoires between all taxa. Differences in shape are more pronounced between taxa with different locomotor repertoires (e.g. humans versus all great apes) and less so between taxa with more similar locomotor repertoires.

Differences in lumbar vertebral shape between humans and great apes are therefore partly related to adaptations to weight transmission through the lumbar spine during locomotion (and posture) and partly to the maintenance of higher degrees of flexion and extension motion of the lumbar spine in humans. In general, this study was able to reproduce the differences in vertebral shape observed between humans and great apes in previous studies. In contrast to those studies, however, details of differences in shape which are related to the orientation of the vertebral arch and the inferior articular processes are more marked. In the following section, the relationship between phylogeny and differences in vertebral size and shape between the taxa is discussed.

4.7.4 Do differences in vertebral size and shape relate to phylogenetic history?

To investigate how differences in vertebral size and shape are related to phylogenetic history, hypotheses 4.1 (vertebral size) and 4.2 (vertebral shape) were formulated.

Hypothesis 4.1 tests for the presence or absence of a significant relationship between inter-specific differences in vertebral size and the currently most favoured model of phylogenetic relationships between the taxa in the study.

Hypothesis 4.2 was formulated to assess the presence or absence of a relationship between inter-specific differences in vertebral shape and the currently most favoured model of phylogenetic relationships.

To address hypothesis 4.1, in analysis 1 differences in vertebral centroid size (calculated in analysis 1) are presented in a two-dimensional phenogram (see figure 4.6) and compared to the phylogenetic tree (figure 4.1). The results from this comparison indicate that differences in vertebral size are smallest between humans and *Gorilla* and between *Pan* and *Pongo*. These results do not reflect the commonly agreed phylogenetic distances between the taxa: *Homo sapiens* is considered to be the sister taxon of *Pan*, and their closest relative is *Gorilla*. All three are close relatives to *Pongo*.

Hypothesis 4.2 is addressed by analysis 5, which provides two-dimensional phenograms for Procrustes distances (representing differences in vertebral shape) between the four taxa at each comparison level (see figure 4.15). These phenograms differ considerably from the phylogenetic tree (see figure 4.1). Therefore, no relationship between phylogeny and differences in vertebral shape is observed.

Hypotheses 1.1 to 4.2 have addressed questions of the presence of relationships between inter-specific differences in vertebral size and shape of single lumbar vertebrae. However, single vertebrae are parts of functional regions of the vertebral column. The analysis of patterns of vertebral size and shape variation along the lumbar spine is of interest because it relates to the function of the lumbar vertebral spine as a whole. Thus, in the following sections results from the analyses of inter-specific differences in patterns of inter-segmental size and shape variation along the lumbar spine are discussed in relation to inter-specific differences in body weight, locomotor repertoires, and phylogeny. Additionally, inter-specific differences between these patterns at different stages of postnatal development (infant, juvenile) will be discussed.

4.7.5 To what extent do patterns of inter-segmental shape variation along the lumbar spine differ between the four hominoid taxa in the study and how are these differences established throughout postnatal ontogeny?

In a first step, the presence of inter-specific differences in metameric patterns of vertebral size and shape variation was explored. Thus, hypothesis 5 was formulated. In the case that hypothesis 5 was falsified (there are inter-specific differences between the patterns of size and shape variation observed between the taxa) these differences were analysed in relation to inter-specific differences in body weight, locomotor repertoires, and phylogeny.

Hypothesis 5 simply addresses the question of presence or absence of inter-specific differences in vertebral size and shape variation patterns along the lumbar spine of adult specimens of reach taxon.

Hypotheses 6.1 to 6.3 were formulated to assess the relationship between the differences in patterns of metameric variation in size and shape and inter-specific differences in body weight, locomotor repertoires, and phylogeny.

Presence of inter-specific differences in size and shape variation patterns

To address hypothesis 5, in analysis 6 the patterns of size and shape variation along the lumbar spine of adult specimens of each taxon were visualized and compared. To visualize patterns of size variation, a scatter plot of vertebral level versus mean vertebral centroid size was produced for each taxon. To assess differences between metameric patterns of vertebral shape variation between the taxa, mean vertebral shape data was analysed with GPA/PCA. The patterns were then visualized by presenting scatter plots of the mean vertebral shape data in three dimensions (PCs 1 vs. 2 vs. 3). The five last presacral vertebrae were considered.

Results indicate that all great apes share a common pattern of vertebral size variation along the lumbar spine. Humans, on the other hand show a different pattern of vertebral size variation compared to all great apes. The similarities between great ape taxa reflect their similar weight transmission mechanisms. The contrast between the patterns of vertebral size variation between humans and great apes, on the other hand, reflects the differences between their weight transmission mechanisms.

The results from the comparison of adult vertebral shape variation, on the other hand, are different from those of vertebral size variation: Patterns of vertebral shape variation differ between humans, *Pongo* and the African apes. They may reflect differences in locomotor repertoires between the taxa.

4.7.6 Inter-specific differences between patterns of vertebral size and shape variation in relation to differences in body weight, locomotor functions, and phylogeny

Body weight and vertebral size and shape

To assess the questions raised in hypothesis 6.1 (the relationship between differences in body weight and patterns of metameric variation in vertebral size and shape), the phenogram depicting distances between vertebral centroid sizes (figure 4.6) is compared with the patterns of vertebral size variation. The results from this comparison indicate that there is no match between differences in body weight and differences in patterns of size variation: Humans and *Gorilla* are closest to each other in vertebral size. The same is observed for *Pongo* and *Pan*. However, comparing the patterns of vertebral size variation between the taxa reveals that humans show a pattern very different from all the great ape taxa. The latter all show similar patterns. Thus there is no relationship between body weight and patterns of metameric variation in vertebral size among living hominoids.

Differences between patterns of vertebral shape variation (results from analysis 6) were compared to differences in body weight between the taxa (results from analysis 1). There is no relationship observed between inter-specific differences in body weight and inter-specific differences in patterns of shape variation.

Locomotor repertoires and patterns of vertebral size and shape variation

Hypothesis 6.2 addresses the question of the presence of a relationship between differences in metameric patterns of vertebral size and shape variation and differences in the locomotor repertoires of the hominoid taxa.

To assess the relationships between differences in patterns of vertebral size variation and differences between locomotor repertoires, results from analysis 6 (differences in vertebral size and shape variation patterns) and analyses 2, 3, and 4 (inter-specific differences in vertebral shape, general assessment, inter-specific differences in vertebral shape between samples of all taxa, and inter-specific differences in vertebral shape between species means) were compared with each other. In the case of modern humans, there is a correspondence: *Homo sapiens* is most different from all great apes both in, patterns of vertebral size variation and locomotor repertoire. There are, however,

differences between the locomotor repertoires of African and Asian great apes that are not reflected in these findings.

The comparison of inter-specific differences in metameric patterns of vertebral shape variation and differences in locomotor repertoires indicates a close relationship between them. In both shape variation and locomotor repertoire, humans are most different from all other taxa, followed by *Pongo*. Between the African ape taxa, the smallest inter-specific differences in patterns of shape variation and locomotor repertoires are recorded.

Phylogeny and differences in vertebral size and shape variation

Finally, a comparison of metameric patterns of vertebral size and shape variation and the phylogenetic tree did not show any relationship between these. Humans are the closest living relatives of *Pan* and both are more closely related to *Gorilla* than to *Pongo*. In the case of metameric patterns of size variation, that of *Pan* resembles those of *Gorilla* and *Pongo* far more than that of *Homo sapiens*. In the case of metameric shape variation, humans are most different from all other taxa and *Pan* resembles *Gorilla* the most. Neither reflects phylogeny.

Summary

Results from the preceding analyses of patterns of single lumbar vertebral size and shape variation are well reflected by the results of the analyses of patterns of vertebral size and shape variation. The exception is that patterns of metameric variation in size do reflect the extreme locomotor adaptations of humans whereas the sizes of single vertebrae do not.

4.7.7 Differences in metameric patterns of variation of vertebral form are established during ontogeny

The questions addressed by hypotheses 1.1 to 6.3 were focused on inter-specific differences in patterns of vertebral size and shape variation between adult specimens. Results clearly indicate that inter-specific differences in locomotor repertoires have a strong relation with differences in vertebral shape and much weaker relationship to vertebral size except in the case of the pattern of metameric size variation of vertebrae in humans contrasted to apes. Either, these differences are established prenatally and

largely under the influence of heritable systems, or they are more mechanically influenced during postnatal growth. It is therefore of interest to see how metameric patterns of vertebral size and shape variation arise during the postnatal growth period, in different taxa. A complete ontogenetic study of how and when inter-specific differences in vertebral size and shape variation patterns are established in the postnatal period is outside of the scope of this study. However, where samples allow differences between patterns of vertebral shape variation are explored between averages of infant and juvenile specimens of each taxon.

The differences between the patterns of vertebral shape variation in samples of infant and juvenile specimens of each taxon were visualized in the same manner as those between the adult specimens (analysis 5). There is a lack of human data, in particular for infants but a single specimen is available. Results from the comparison of metameric patterns of vertebral form variation between these age groups indicate that it is likely humans from a very early age are distinct from all great ape taxa. Tentatively, given the sample of one individual it appears that the infant human pattern might already manifest the characteristic differences in shape between the two last presacral vertebrae and L1 to L3 that distinguish adult humans from apes. Pattern differences between humans and great apes become more accentuated in juveniles.

The comparison of infant patterns of shape variation among great apes shows that *Pongo* is more similar to the African apes at this stage in the postnatal period. The similarities between patterns of vertebral shape variation are larger between juvenile African and Asian apes than between adult ones.

These findings suggest that among the great ape taxa, distinctions in patterns of metameric variation of vertebral shape, to some extent, arise postnatally. This implies that, at least in part, the mechanical environment in which the vertebrae develop influences the subsequent development of differences in form.

In humans the findings are much more tentative given the single available infant. However, the pattern of vertebral shape variation observed in this infant is very similar to that observed in adult *Homo sapiens*. In combination with the findings from the exploration of the juvenile human material, this implies that the human pattern of vertebral metameric shape variation differs from those of great apes from an earlier

stage in ontogeny. Thus, there is the possibility of greater genetic influence in determining the differences between adult humans and apes.

4.7.8 Summary

Of the three factors investigated in the present study (inter-specific differences in body weight, locomotor patterns, and phylogeny), body weight differences and locomotor repertoire differences show a relationship with differences in vertebral size and shape, whereas phylogeny does not.

However, body weight and locomotor repertoires differ in the ways they impact on vertebral size and shape: Between all great apes, a strong, positive relationship was observed between differences in body weight and in vertebral size. Large apes (*Gorilla*, *Pongo*) have larger lumbar vertebrae than does the small ape *Pan*. Humans deviate from this in that their lumbar vertebrae are larger than would be expected for a hominoid of their weight. This discrepancy is related to the differences in weight transmission mechanisms between great apes and humans, due to bipedal gait in the latter.

In contrast to inter-specific differences in body weight, those in locomotor repertoires have a strong correlation with vertebral shape between all taxa. The most significant differences in vertebral shape are observed between humans and all great apes followed by those between Asian and African apes. Between the African apes, the smallest differences in vertebral shape are observed. Of the hominoids in the present study, humans have the longest and most flexible lumbar spine. This is regarded as an adaptation to their bipedal locomotion. Differences in vertebral shape between humans and great apes are likely adaptations to differences in weight transmission and differences in spinal mobility. Differences in vertebral shape between *Pongo* and African apes are highly likely attributable to the differences in locomotion.

4.8 Conclusions

4.8.1 Single lumbar vertebral shapes reflect locomotor functions

By and large, the investigation of the shape of a single lumbar vertebra reveals important information about locomotion. That this is indeed the case across a range of

mammals has been shown e.g. by Boszczyk et al. (2001) and Slijper (1946). In contrast studies of the sizes of single lumbar vertebrae are uninformative about locomotion.

In modern humans, and presumably other hominin bipeds, the last lumbar vertebra is the most different when compared to other primates and that this is highly likely due to adaptations to upright trunk posture and bipedal gait (Boszczyk et al., 2001; Rose, 1975; Sanders, 1998; Schultz, 1950a; Shapiro, 1993a; Slijper, 1946). Results from the present study confirm these results – differences between all great ape taxa and modern humans are greatest at comparison level 4 (last lumbars) for single vertebral shapes, species mean shapes and in the comparison of patterns of shape changes along the lumbar spine.

4.8.2 Single vertebral comparison vs. size and shape changes along the lumbar spine – same results or different?

This study explored inter-specific differences in vertebral size and shape between single lumbar vertebrae as well as inter-specific differences in patterns of inter-segmental shape variation along the lumbar spine. As seen earlier in the study, results from analyses of single lumbar vertebral shape and from the analysis of patterns of inter-segmental shape variation along the lumbar spine are very similar. In both cases, humans have the most different lumbar vertebrae from all great apes followed by *Pongo*. In contrast, the African apes have relatively similar single lumbar vertebrae and share a pattern of shape changes along the lumbar spine.

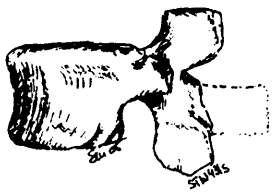
With regard to size and in contrast to analyses of single vertebrae where body weight is correlated with vertebral size but not locomotor adaptation, analyses of metameric size variation indicate that humans differ from apes in a way that reflects bipedal posture and locomotion. Thus in humans but not in apes there is marked gradation of vertebral sizes in the lumbar spine from small to large in the cranio-caudal direction.

4.8.3 Implications for studies of fossil lumbar vertebral material

If locomotor functions are the predominant external influence on lumbar vertebral shape of most recent hominoid taxa (*Hylobates* was not studied here), then lumbar vertebrae are an informative part of the postcranium that potentially can reveal information about the locomotor functions of a given species without too much background noise

attributable (but hardly separable) from other external factors such as body weight or phylogeny.

Further, that a single lumbar vertebra might be sufficient for a relatively good prediction as to what locomotor patterns contributed to the locomotor repertoire of a fossil has interesting implications for the study of hominin evolution. First, if reliable predictions about the locomotion of fossil hominins is possible from only a few surviving vertebrae, this facilitates the study of their locomotion considerably. Second if one is concerned to consider if a particular fossil hominin locomotor repertoire included considerable amounts of bipedalism, the last lumbar vertebra is particularly informative. In the following chapter fossil lumbar vertebrae are compared with those of living hominoids. The analyses will build upon the information gleaned from the studies of Chapters III and IV.



CHAPTER V, FOSSIL SHAPE VARIATION

The lumbar spine of *Australopithecus africanus* reflects a unique locomotor repertoire – closest probably to those of *Homo sapiens* and to a lesser degree *Pongo pygmaeus* but very different from the African apes *Gorilla gorilla* and *Pan troglodytes*

5.1. Introduction

In this chapter, differences in lumbar vertebral shape between fossil hominin taxa and the modern hominoid taxa (*Pan, Gorilla, Pongo*, and *Homo sapiens*) will be explored. In Chapter I, the issue of the role of bipedalism in the locomotor repertoire of fossil hominins as well as potential differences in the biomechanics of their bipedal gaits were introduced. In this chapter differences in shape of the fossil lumbar vertebrae when compared to modern hominoid taxa will be assessed and the results will be discussed in relation to the preceding review. These comparisons will be conducted for single lumbar vertebrae as well as for patterns of vertebral size and shape variation along the lumbar spine. This present study attempts to explain the results (intra-specific differences in vertebral size and shape) from analyses of vertebral size and shape in the context of differences in body weight and locomotor functions. This is because results from Chapter IV (inter-specific size and shape variation between modern taxa) show, that body weight is the most important factor to impact upon vertebral size and locomotion on shape between the modern taxa. In hominoids phylogeny does not have a relationship with differences in vertebral size and shape at all. Thus, in the present study of fossil hominin vertebral size and shape, the focus is on differences in vertebral size and shape in relation to differences in body weight and locomotor repertoires only. More specifically, in this present study, the focus is on hindlimb use in locomotor repertoires of fossil hominins, particularly in relation to their adaptations to some form of bipedal gait.

To further facilitate the introduction of this chapter, the results of Chapters III and IV are briefly summarized and presented in relation to the questions addressed. In addition, a brief overview of current opinions about the function and adaptation of the lumbar spine in australopithecines and *Homo ergaster* as well as their locomotor repertoires and

the degree of bipedalism expressed by each taxon are presented below. This section is then followed by the questions and hypotheses that will be further addressed in this chapter.

The results from the chapters addressing intra- and inter-specific differences in vertebral size and shape of modern hominoid taxa revealed that the inter-specific differences in vertebral shape are highly influenced by locomotor functions. Based on molecular data, the African ape taxa are not considered to be each other's closest relative. Nevertheless, their lumbar vertebrae are more similar in shape to each other than are the vertebrae of humans and chimpanzees, which supposedly are closest living relatives (supported by molecular data). At the level of intra-specific size and shape variation, differences in vertebral shape between the sexes in the highly size dimorphic *Gorilla* are closely linked to differences in body weight. Although humans are less dimorphic in size than the large apes, the magnitude of differences in shape between the sexes far exceeds that observed in *Gorilla*. In the case of modern humans, upright trunk posture, and habitual bipedal gait, and sexual dimorphism in pelvic and sacral morphology are related to the sexual shape dimorphism. Since permanently upright body posture and habitual bipedalism shape modern human vertebrae, it will be interesting to investigate if the same features are observed in the australopithecine material. An attempt will be made to interpret the australopithecine vertebral shape in relation to locomotor function.

5.1.2 Background

5.1.3 What role does bipedalism play in the locomotor repertoire of the fossil taxa?

In the introductory chapter, the australopithecine postcranial adaptations to bipedalism and arboreal locomotion and the shift in their perception and interpretation throughout the last decades has been discussed. In general, the australopithecine postcranium of both East and South African and robust and gracile taxa seem to be quite similar to each other – despite some considerable differences in size and differences observed betsen individual fossil specimens. Thus, in the following section a brief overview for each of the taxa as well as a comparison of *A. afarensis* with *A. africanus* is presented.

Australopithecus afarensis

The postcranium of *A. afarensis* presents a mosaic mixture of adaptations to a habitual form of bipedalism and more ape-like features which indicates an ongoing reliance on forms of arboreal locomotion. The lower limbs of *A. afarensis* in particular show adaptations to bipedalism (Berge, 1994; Häusler and McHenry, 2004; Latimer, 1991; McHenry and Berger, 1998; Stern and Susman, 1983). The pelvis combines more ape-like features with more human-like ones. The latter include a short ilium, a sciatic notch, an anterior inferior iliac spine and a wide sacrum (Häusler, 2001; Häusler and Schmid, 1995; Rak, 1991; Schmid, 1991). Furthermore, the large femoral bicondylar angle (= degree of obliquity of the femoral shaft) - in australopithecines it is as large or exceeds that of modern humans (Stern and Susman, 1983) - and the human-like elliptical profile of the lateral femoral condyle (Heiple and Lovejoy, 1971) are among adaptations of the australopithecine femur to bipedal gait (this does not contradict the presence of several features of the australopithecine femur which are uniquely australopithecine in nature or features which are best explained in relation to arboreal locomotion). The feet again express a mosaic of features such as an adducted hallux and robust calcaneal tuberosity with relatively short toes which are similar to those of modern humans (Harcourt-Smith and Aiello, 2004). Yet the phalanges are curved and the shape of the talus is more ape-like (Stern and Susman, 1983). In contrast, the upper limbs show more ape-like than human-like features. Although relatively shorter than in great apes, the upper limbs of *A. afarensis* are longer than those of modern humans (McHenry, 1986; McHenry and Berger, 1998; Schmid, 1983; Stern and Susman, 1983). The elbow and wrist joints are more ape-like as is the orientation and shape of the scapula (Schmid, 1983; Stern and Susman, 1983; Stern et al., 1984; Vrba, 1979). The trunk is relatively short and the thorax shows an inverted funnel-shape – similar to that observed in great apes (Schmid, 1983). Also, body proportions generally differ from modern humans and are somewhat more ape-like. Australopithecines have a relatively short trunk, short legs, and long arms (Jungers, 1983; Jungers, 1988; McHenry and Berger, 1998; Stern and Susman, 1983). Current opinions tend to acknowledge that the locomotor repertoire of *A. afarensis* consists of a mixture of bipedal gait and arboreal locomotion (Latimer, 1991; Schmid, 1983; Stern and Susman, 1983; Stern et al., 1984; Ward, 2002). However, biomechanics of the *A. afarensis* bipedal gait and how much arboreal locomotor patterns contribute to the *A. afarensis* locomotor repertoire is still not resolved.

Australopithecus africanus

The postcranium of *A. africanus* is deemed to be similar to that of *A. afarensis* (Häusler, 2002; Lockwood and Tobias, 1999; McHenry, 1986; McHenry, 1994; Toussaint et al., 2003). However, there are significant differences in the shape and size of the skull and the dentition between the two taxa that justified the description of the new taxon *A. afarensis* (Johanson et al., 1982a; Johanson et al., 1982b; McHenry, 1986) from the findings from East Africa. For almost 40 years, *A. africanus* was considered a habitual biped (Broom, 1938a; Dart, 1925; Robinson, 1972). However, that australopithecines were exclusive bipeds has been subject to doubt (Ashton and Zuckerman, 1956a; Oxnard, 1975; Zuckerman et al., 1973). Vertebrae of *A. africanus* are relatively scarce. Until very recently only the partial vertebral column of specimen Sts14 was available. However, newly available fossil material such as specimens Stw8, Stw572, and most importantly the complete lumbar vertebral series of Stw431 allow a more extensive comparison of *A. africanus* with modern taxa and this also helps to better demonstrate the variability within *A. africanus*.

5.1.4 Differences in bipedal locomotion between *A. afarensis* and *A. africanus*

Some disagreement about the similarity of the postcranium of *A. africanus* and *A. afarensis* was voiced by McHenry and Berger (1998) who compared the size of joints (hip, knee, shoulder etc). They conclude that *A. africanus* is probably more ape-like in its body proportions than *A. afarensis*. This is because in *A. africanus*, the forelimbs are much larger and longer than the hindlimbs. However, these results have been questioned by Häusler (2002). Based on his comparative analysis of the *A. africanus* and *A. afarensis* pelves, he could not support the differences in body proportions of the two taxa found by McHenry and Berger (1998). Most importantly, Häusler could not exclude that *A. africanus* used arboreal locomotion. The findings of Harcourt-Smith (2002) point in the same direction: The foot morphology of *A. afarensis* and *A. africanus* differ somewhat from each other, yet both show adaptations toward a form of bipedalism (probably different from modern humans). At the same time, they retain features that would facilitate arboreal locomotion. This would indicate different distinct adaptations to increased bipedal locomotion in these hominins but as homoplasies to the adaptations seen in modern humans.

Homo ergaster

Generally, there is little doubt about the locomotor repertoire of *Homo ergaster*. KNM-WT15000 represents the oldest and most complete skeleton of a hominin with modern human body proportions, including a barrel-shaped thorax, a narrow pelvis with laterally orientated short iliac blades (Ruff, 1996; Walker and Ruff, 1993), relatively long legs, and relatively short arms (Ruff and Walker, 1993). Nevertheless, there are some differences observed in body proportions between *Homo ergaster* and modern humans: *Homo ergaster* probably had shorter arms in relation to leg length and a shorter trunk than that modern humans (Brown et al., 1985; Wang et al., 2004). However, these differences in body proportions as yet remain to be interpreted in relation to the age (juvenile) of the particular *Homo ergaster* specimen and in relation to the specific postnatal growth patterns of various postcranial regions (e.g. legs, arms, trunk). The general opinion holds that the biomechanics of the bipedal gait of this taxon are similar to those of modern *Homo sapiens*. The relatively long legs in particular (compared to *Australopithecus*) suggest the ability for long stride length during walking (and running) (Bramble and Lieberman, 2004; McHenry, 1991a; Wang et al., 2004). Thus, the *Homo ergaster* locomotor repertoire is highly likely to have consisted exclusively of modern human type bipedal gait and to have also included long distance ranging and running (Bramble and Lieberman, 2004; Rose, 1991).

5.1.5 The morphology of the australopithecine lumbar vertebrae

The dispute over the locomotor repertoire of australopithecines is also reflected in the analysis of the fossil vertebral material. There is a "parallel evolution" observed with regard to how the fossil vertebrae are interpreted, mirroring current opinion on australopithecine bipedalism at a given time.

In 1972, Robinson described and interpreted the vertebrae of the partial *A. africanus* skeleton Sts14 as very much resembling modern humans - despite the comparatively small size of the specimen. According to Robinson, the *A. africanus* lumbar vertebrae indicate that a lumbar lordosis was present because the vertebral bodies exhibit posterior wedging and the sacrum is positioned within the pelvis in a way that would encourage the presence of a lumbar lordosis. Also, the lumbar spine was highly flexible because of the high number of lumbars (Robinson counted six vertebrae) which are both distinctively human-like characteristics. Robinson stressed similarities between humans

and *A. africanus* are greater than the findings which set the two taxa apart. Among these are the relatively small lumbar vertebral bodies of Sts14 compared to modern hominoids – in fact, Sts14 seems to have smaller lumbar vertebral bodies than any of the modern great apes. Also, costal processes appear to be relatively longer in *A. africanus* than in any of the modern great apes or *Homo sapiens*.

A few decades later, Sanders (1998) concluded that australopithecines (*A. africanus* and *A. afarensis*) – although they resemble humans the most - are different from both modern humans and modern apes. Sanders, writing later, had the advantage of a larger *A. africanus* vertebral sample consisting not only of the Sts14 specimen but also of specimens Stw8 (a partial lumbar vertebral series) and Stw41 (a partial thoracic vertebral series) which are considered to belong to the same specimen. Based on this sample, he also concluded that the lumbar vertebrae of the various specimens were not very similar to each other. In contrast to Robinson's emphasis on the more human-like features of Sts14, Sanders stresses the features which set humans and australopithecines apart: the relatively smaller vertebral bodies, the short, broad "*hyper-human*" (Sander's word) pedicles, the relatively longer spinous process and the relatively larger articular processes and joint facets (especially the relatively large superior articular processes). Sanders concludes that the lumbar vertebrae of australopithecines show no adaptation to quadrupedal gait as seen in the African great apes. There is no imprint of climbing behaviour seen in the australopithecine lumbar vertebrae either, as their long flexible lumbar spine is not suited to climbing behaviour. The weight bearing mechanism through the lumbar spine in australopithecines is considered to be very different from that observed in modern humans because the vertebral bodies are very small and the processes and vertebral arches are relatively large. Thus, australopithecines probably transmitted larger proportions of body weight through the vertebral arch and articular joints rather than through the vertebral bodies.

The studies by Ruff and Walker (1993) and Sanders (1998) contradicted results from a study of the pedicle size and shape of *A. africanus* (based on specimen Sts14 only) in relation to modern hominoid taxa conducted by Shapiro (1993a). According to Shapiro, the pattern of pedicle size and shape variation along the lumbar spine – especially in the last lumbar vertebra of Sts14 does not resemble the pattern seen in modern humans. Sanders found this not to be true in *A. africanus* in general but had to admit that the Sts14 specimen is somewhat of an exception to this.

The latest discovery of an *A. africanus* lumbar vertebral series, Stw431, as well as that of Sts14 were exhaustively compared with modern humans, and one specimen each of *Gorilla*, *Pan*, and *Pongo* by Benade (1990). Her conclusions include the presence of a lumbar lordosis in Sts14 and Stw431. Also, that the size, shape, and orientation of the articular facets of both, Sts14 and Stw431, resemble modern humans most. She also concludes – based on the overall adaptations observed in the lumbar spine of *A. africanus* that its bipedal gait resembles that of modern humans.

In the case of *A. afarensis*, Cook (1983) found their lumbar vertebrae to resemble humans more than those of African great apes or any of the non-human primates. Nevertheless in *A. afarensis* too, some morphological features deviated quite clearly from the human condition. *A. afarensis* has relatively small vertebral bodies and relatively longer vertebral processes than humans.

To date, most researchers of the hominin vertebral column agree that the australopithecine lumbar vertebrae closely resemble *Homo sapiens*. Nevertheless, australopithecine vertebrae are not identical to those of modern humans and show a unique mixture of features, such as the relatively small vertebral bodies and long vertebral processes which are not seen in any of the modern hominoid taxa. In contrast to these findings in the lumbar spine, the australopithecine thoracic spine seems to resemble that of great apes more than that of modern humans (Sanders, 1998; Schmid, 1991).

5.1.6 The morphology of the *Homo ergaster* lumbar vertebrae

The *Homo ergaster* lumbar vertebrae are "*strikingly similar to humans*" (Latimer and Ward, 1993) in nearly all aspects which are significantly related to the vertebral column's adaptation to bipedal gait: *Homo ergaster* lumbar vertebrae show evidence for the presence of a lumbar lordosis. Vertebral body shape, inter-articular facet distance variation patterns, and the orientation of the spinous process are all very similar to modern humans. However, some differences in vertebral shape are noted between the two *Homo* taxa: Latimer and Ward (1993) report relatively smaller vertebral bodies in *Homo ergaster* when compared to modern humans. Brown et al. (1985) also report longer spinous processes in the *Homo ergaster* specimen than in modern humans. However, this finding was not confirmed by Latimer and Ward but Sanders (1998) also

found relatively smaller vertebral bodies and relatively longer vertebral processes in the KNM-WT 15000 specimen. Sanders notes that australopithecines and *Homo ergaster* resemble each other in these features. Nevertheless, current opinion tends to see *Homo ergaster* as a *Homo sapiens*-like biped with the same adaptations to locomotion as seen in modern humans (Bramble and Lieberman, 2004). These findings are corroborated by the results of a study of the dimension of the *Homo ergaster* vertebral canal (MacLarnon, 1993). They indicate that the vertebral canal dimensions as well as the patterns of dimension variation along the vertebral column vary in similar ways. The variation of vertebral canal dimensions are singular in modern *Homo sapiens* and are seen in relation to dominant hindlimb enervation, presumably due to bipedal gait (MacLarnon, 1995). Interestingly, the *Homo ergaster* specimen KNM-WT 15000 seems to deviate from the pattern of modern human vertebral canal dimension variation in the thoracic section of the vertebral column (MacLarnon, 1993). However, these differences probably reflect differences in breath control related to speech abilities between *Homo ergaster* and *Homo sapiens* (MacLarnon, 1993; MacLarnon and Hewitt, 2004).

5.1.7 Did the spine of fossil taxa adapt to bipedalism in different ways than the human spine? – Evidence from other postcranial elements

Differences in body proportions between modern humans and australopithecines and the mosaic combination of human, ape-like and unique australopithecine features in the fossil hominin postcranium indicate that there are not only differences in the locomotor repertories between humans and australopithecines but also in the biomechanics of the bipedal gaits. Body proportions and trunk morphology of australopithecines are considered to be good indicators that the australopithecine bipedal gait lacked distinct adaptations to energetically efficient long distance walking and more importantly to running as seen in modern humans (Berge, 1984; Berge, 1994; Bramble and Lieberman, 2004; Harcourt-Smith and Aiello, 2004; Oxnard, 1975; Ruff, 1996; Ruff and Walker, 1993; Sanders, 1998; Schmid, 1991; Tardieu, 1997; Tardieu et al., 1993; Wang et al., 2004; Zuckerman et al., 1973).

5.1.8 The comparison of single vertebrae vs. the lumbar spine as a functional unit

In the present study, single vertebrae of different taxa will be compared to each other. This in general will be a repetition of earlier studies. However, since previous studies

have been conducted by Benade (1990), Robinson (1972), and Sanders (1998), additional fossil material has become available for comparative studies including *A. africanus*. Among others, the new material also contains a complete lumbar vertebral series (Stw431). The comparison of this extended *A. africanus* sample with modern hominoid taxa allows a direct comparison of vertebral shape variation along the lumbar spine (from L1 to L5). This might shed light on the role of the australopithecine lumbar spine in bipedal locomotion when compared to that of modern humans.

5.2. The aims of the present study

This study provides the first comprehensive three dimensional morphometric assessment of fossil hominin lumbar spines in relation to modern hominoid taxa. The aims of the studies presented in this chapter are first to assess the variations between australopithecine fossils to determine if they are consistent with the current view of two species, *A. africanus* and *A. afarensis*, and second to assess the similarities and differences between the fossils and modern taxa. The preceding chapters have served to indicate that inter-specific differences in size and shape between lumbar spines principally provide information about locomotor differences. Thus the relationships of the fossils to modern species will be of interest from the point of view of assessing the locomotor repertoires of the fossils.

In contrast to the previous chapters, where the aims have been addressed by formulating hypotheses, the present study is more descriptive. This is because the locomotor repertoires and body weight of australopithecines are not known with certainty. The discovery of new information relating to this is an aim of this study. Additionally the samples of fossil taxa are small, severely limiting the possibility of statistical testing of the significance of differences in size and shape.

The specific aims are summarized as follows:

1. To assess the variability in size and shape in the lumbar vertebral column of *Australopithecus* relative to that found in modern taxa

2. To assess the differences in size and shape between the fossil hominin taxa *A. africanus*, *A. afarensis,* and *Homo ergaster* and the modern taxa *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes,* and *Pongo pygmaeus*
3. To relate any differences in size and shape between fossils and between fossils and modern taxa the currently held views on their locomotor repertoires

These assessments are carried out through a series of analyses that examine the following:

1. Vertebral size variability between and within modern species in relation to vertebral size variability within and between fossil species.

2. Vertebral shape variability between and within modern species in relation to shape variability within and between fossil species

3. Patterns of vertebral size and shape variation along the lumbar spine between and within modern species in relation to patterns of vertebral size and shape variability within and between fossil species

The methods used are those of geometric morphometrics as described previously in Chapter II (materials and methods) and employed in Chapters III (intra-specific size and shape variation in modern taxa) and IV (inter-specific size and shape variation between modern taxa). The results obtained are placed in the context of the current literature in the discussion section of this present chapter.

5.3. Materials

The detailed description of the materials utilized in the present study is summarized in Chapter II materials and methods (from p. 94) In the following section only a brief summary of the recent as well as the fossil material is presented.

Recent hominoid taxa

The comparative sample of modern taxa is the same for *Gorilla, Pan*, *Pongo*, and *Homo sapiens*, as was utilized in the preceding chapters that investigated intra- and inter-specific size and shape variation (Chapters III and IV). The recent hominoid sample,

separated into taxa, sex, and age sub-samples has been introduced previously in Chapter II materials and methods (pp. 95-100, tables 2.1 and 2.2). In the case of comparative analyses between modern taxa and the *Homo ergaster* specimen, modern comparative material was drawn from the juvenile and infant samples because the only available *Homo ergaster* specimen is of juvenile age.

Fossil hominids

The fossil material investigated in the present study is introduced and described in Chapter II, materials and methods (pp. 100-107, tables 2.3 to 2.5). In summary, the fossil sample consists of twelve lumbar vertebrae from four specimens ascribed to *A. africanus*, one lumbar vertebra from an *A. afarensis* specimen, and four lumbars from a *Homo ergaster* specimen. The four specimens of *A. africanus* consist of two complete lumbar series (specimens Sts14 and Stw431) and two isolated lumbar vertebrae (specimens Stw572 and Stw8). Specimen Stw8 is not a single lumbar vertebra but part of a vertebral series. However, only one vertebra of that series was sufficiently well preserved for the collection of three-dimensional landmarks. Table 5.1 summarizes the fossil material as well as the landmarks which were located on reconstructed elements of the fossil vertebrae. The appendix (pp. 389-406) visualizes the reconstructions conducted on each fossil vertebra. Chapter II (material and methods) also provides a description of the various fossil vertebrae and indicates the state of preservation of each of the vertebrae. Reconstruction techniques used on the fossil vertebrae are also described in Chapter II. Some of the fossil specimens exhibited pathology (*Homo ergaster*; all lumbars; *A. africanus;* Stw431, L4 and L5). These specimens still were included because the sample of fossil vertebrae available is small at best.

Specimen	Vertebra	Reconstructed landmarks
AL288-1	probably L3 or L2?	29, 35
A. africanus Sts14	L1	28, 30-32, 43, 45, 46, 49, 50, 52, 53, 58-61
A. africanus Sts14	L2	35
A. africanus Sts14	L3	**5, 6,** 12, 13, **18-20**, 35-37, 39-42, 50, 53-55
A. africanus Sts14	L4	**1-3**, 10-13, **18-20**, 26, **29**, 33, 35, 47, 50, 53, 54, 57-62
A. africanus Sts14	L5	11-13, 19, 20, 24, 37, 49, 50, 52-56, 58-62
A. africanus Stw431	L1	25, 27-29, 33-46
A. africanus Stw431	L2	12, 13
A. africanus Stw431	L3	9, 12-14, 22, 23, 27-32, 34-36, 49-51
A. africanus Stw431	L4	9, 23, 24, 27-32, 35, 39-42, 47, 48, 58-62
A. africanus Stw431	L5	5-8, 10, 12, 13, 18-21, 25, 26, 33-38, 43-46, 48-50, 57-62
A. africanus Stw8	L2?	9, 12, 13, 27-32, 35, 39-42, 47, 50, 51-55
A. africanus Stw572	L4?	5-7, 12, 13, 19, 23, 28-33, 35-37, 39-42, 50, 53, 54
Homo ergaster KNM-WT 15000 BA, AR	Th12	6, 7, 9, 10, 12-14, 22, 23, 25-47, 49-57
Homo ergaster KNM-WT 15000 AV, AA	L2 new*: L1	3, 4, 6, 7, 10, 12, 13, 20, 21, 27, 29-33, 35, 50, 58-62
Homo ergaster KNM-WT 15000 AB	L3 new: L3	2-7, 10, 20, 29, 33-35, 43-46
Homo ergaster KNM-WT 15000 BM	L4 new: L4	2, 15, 18, 29
Homo ergaster KNM-WT 15000 AC	L5 new L5	none

Table 5.1 Summary of fossil hominid taxa examined in the fossil study. In the case of *A. africanus* Sts14: landmarks are reconstructed by Robinson (1972), except for bold script ones. These were sampled directly on the CT-reconstructions of the relevant lumbar vertebrae. * see Häusler et al. (2002)

5.3.1 Methods - general

As in the previous two studies on intra- and inter-specific vertebral size and shape variation (Chapters III and IV), the form of each of the last five consecutive presacral vertebrae of each specimen was recorded as sets of three-dimensional landmark

configurations, consisting of 62 bony landmarks. For detailed information on data collection technique and a complete list of the landmarks used in the present study see Chapter II (pp. 107-114). In the case of damaged or only partially preserved fossil vertebrae, reconstructions were made to guarantee the collection of all 62 landmarks.

Due to the small sample size of fossil material, the possibilities to apply statistical tests to test impressions of similarity and difference are somewhat reduced when compared to the previous studies of modern hominoid vertebral material. The main method employed to analyse the landmark data was again GPA/PCA. Supplementary methods consist of matrix correlation (using Euclidean distances) on Procrustes distances to assess differences in shape between taxa, and the production of UPGMA phenograms to visualize shape differences between taxa. These methods are described in more detail in Chapter II material and methods (pp. 123 onward).

Vertebral comparison levels

Like modern humans, all fossil taxa in this study are considered to possess five lumbar vertebrae (see Chapter I, for further details on the issue of number of lumbar vertebrae in fossil hominins, pp. 72-75). Thus, in the case where fossil taxa were compared to modern humans only, a direct comparison of identical lumbar vertebrae (e.g. L3 with L3) was possible. In the case where fossil hominins were compared to modern great apes, the same five comparison levels as were defined in Chapter IV (pp. 233-235) were employed:

Level 1, solution 1 compares **L1** of humans and fossil hominins with **L1** of great apes
Level 1, solution 2 compares **L2** of humans and fossil hominins with **L1** of great apes
Level 2 compares **L3** of humans and fossil hominins with **L2** of great apes
Level 3 compares **L4** of humans and fossil hominins with **L3** of great apes
Level 4 compares **L5** of humans and fossil hominins with **L4** of great apes

5.3.2 Analyses of vertebral size and shape variation

In order to assess the vertebral size and shape variation within and between modern hominoid taxa this study presents **six analyses** which are as follows:

Analysis 1, intra and inter-specific differences in vertebral size

This analysis assesses the variation in vertebral size between the fossil hominin taxa and between the fossil taxa and the modern hominoids. In a first step, the differences in vertebral size between fossil taxa and modern hominoids are assessed. Thus, species mean size, standard deviation, and the 95% confidence limits (2 sds added and subtracted to species mean serve as proxy for the 95% confidence interval) for both sexes of modern hominoid taxon are calculated at each comparison level. These values (and the 95% confidence limits) are then compared to single fossil vertebrae or where several specimens are available, to fossil mean sizes at each comparison level. This comparison allows assessments of whether the size of fossil vertebrae lies within or outside the vertebral size ranges of various modern hominoid taxa. Simultaneously, this comparison allows the exploration of differences in vertebral size between the fossil taxa. Since there has been a suggestion that the specimens in this study which represent *A. africanus* may in fact include males and females, a further analysis examines the differences in vertebral centroid size between the putative sexes of *A. africanus* in relation to the differences between sexes as found in modern hominoid taxa (see Chapter III). To be able to compare sexual dimorphism in body weight of *A. africanus* with that of the modern taxa, body weight estimations for *A. africanus* have been compiled from the literature. The most commonly agreed estimations are calculated by McHenry (1992a,b) and displayed in table 5.1. From the weight estimations of McHenry, the ♂/♀ weight ratio has been calculated (note that it is equal to that calculated for *Pan*)

Taxon	Female	Male	♂/♀ weight ratio
Homo sapiens	**55** ± 4.62 (1sd = 2.31)	**68** ± 15.5 (1sd = 7.75)	**1.2**
Gorilla gorilla	**91.4** ± 23.6 (1sd = 11.8)	**177.8** ± 47.2 (1sd = 23.6)	**1.95**
Pan troglodytes	**38.1** ± 5.0 (1sd = 2.5	**49.2** ± 9.8 (1sd = 4.9)	**1.3**
Pongo pygmaeus	**38.2** ± 3.0 (1sd = 1.5)	**75.7** ± 10.0 (1sd = 5.0)	**2.0**
A. africanus	**30.2**	**40.8**	**1.3**

Table 5.1 Male and female hominoid body weights in kg. ♂/♀ weight ratio in %.Values are compiled from the following sources: Delgado and Van Schaik (2000), Jungers (1985a), MacKinnon (1974), McHenry (1992a,b), Novak (1999), Plavcan and Van Schaik (1997), Rowe (1996), and Ruff (1991)

Analysis 2, intra and inter-specific differences in single vertebral shape between modern and fossil taxa at various comparison levels

The aim of analysis 2 is to assess differences in vertebral shape between fossil and modern taxa and between the fossils. The choice of analysis is GPA/PCA on single vertebral shapes, performed at various comparison levels. In a first step, the complete australopithecine sample is analysed in order to obtain an estimation of the proximate shape variation to be expected between the australopithecine specimens when later compared to the modern taxa. In comparing modern taxa with fossil hominins, the analysis consisted of GPA/PCA on single lumbar vertebrae of fossil and modern taxa at each comparison level. This was performed in order to assess the relations of the fossil shapes to scatters of shape variation of modern hominoid taxa. In a final step, *Homo ergaster* vertebrae were compared separately to full samples (containing all age groups – infants, juveniles, sub-adults, and adults) of each modern taxon. Scatter plots of PCs, extracted from GPA/PCA on the full sample data and of centroid size vs. PC scores were produced in order to assess the relationship of *Homo ergaster* to modern taxa as well as its position in relation to different age groups.

Analysis 3, exploring inter-specific differences in species mean shapes

Since analyzing whole samples (analysis 2) results in a high dimensional shape space and differences between taxa are to some extent obscured by differences in intra-specific shape variation, analysis 3 of species mean shapes was conducted. This reduces dimensionality and allows direct comparison of differences in shape between species means. Analysis 3 comprises the examination of inter-specific differences in mean shape between modern and fossil taxa. Thus, means of means (= means of the mean at each vertebral level), representing species mean lumbar vertebral shapes, were calculated for the modern taxa and *A. africanus*. GPA/PCA on these data produced scatter plots of species means in three dimensions. To visualize differences in vertebral shape between the taxa, direction and distance from the centroid (calculated from all species means in the analysis) was indicated by lines. In the case where the *Homo ergaster* mean shape was compared with modern means, these were calculated excluding the second lumbar as this vertebra is missing in *H. ergaster*. The comparison of *A. afarensis* also required some adaptations: since the sample of *A. afarensis* consists of a single lumbar vertebra, it was compared with species means of other taxa at comparison level 2 only.

Analysis 4, Procrustes distances between means of means of fossil and modern taxa

Analysis 3 yields information about the relationship between species means of fossil and modern hominoid taxa. Thus, in analysis 4, an attempt is made to quantify the differences in species mean between fossil and modern taxa and between fossil taxa. In analysis 4, Procrustes distances are calculated between species means. The Procrustes distances completely represent the differences between mean shapes. The Procrustes distances are used to produce UPGMA phenograms to visualize in 2D the high D distances between species means. In analysis 4, the same comparisons are made as were in analysis 3. They include the comparison of each of the australopithecine taxa with all modern hominoids, the comparison of both australopithecine taxa with all modern hominoids, and the comparison of *Homo ergaster* with juvenile means of the modern hominoids. To assess differences between species means between the fossil taxa, a comparison was conducted between both australopithecine taxa and *Homo ergaster*, and the modern hominoids. Any comparison that included *A. afarensis* was solely conducted at comparison level 2 (comparing species means at level L2 and L3 respectively). Any comparison that included *Homo ergaster* required the calculation of species means from which L2 was excluded.

Analysis 5, description of differences in shape between modern hominoid taxa and fossil hominins

Analysis 5 produces qualitative descriptions of differences in shape between some modern hominoid taxa and the fossil hominins. Differences in shape between species means are visualized by using grids and distortions thereof on GPA/PCA analysed species mean data. The grid distortions represent differences in shape between the taxa. The grid distortions are calculated with thin spline techniques (see Chapter II, pp. 227-228).

Analysis 6, assessing differences in patterns of vertebral size and shape variation along the lumbar spine between modern and fossil taxa

Analyses 1 to 5 investigate the differences in vertebral size and shape between fossil taxa and fossil and modern hominoid taxa in single lumbar vertebrae. Analysis 6 on the other hand assesses patterns of inter-specific differences in vertebral size and shape along the lumbar spine between modern and fossil taxa. The patterns are examined relatively simply. In the case of metameric patterns of vertebral size variation, a scatter plot of vertebral level (L1, L2,..) versus mean centroid size of each vertebra is produced.

Patterns are visualized by connecting consecutive vertebral levels with lines. Metameric patterns of vertebral shape variation are examined using GPA/PCA of mean vertebral shapes at each comparison level. Patterns are then visualized in two- and three-dimensional scatter plots of PCs. As in the case of patterns of size variation, neighbouring vertebral levels are connected with lines. Where the *Homo ergaster* specimen KNM-WT 15000 is compared with other taxa, some adjustment has to be made for its missing second lumbar vertebra. Thus in these analyses the comparative samples of modern taxa and other fossil hominins omit L2. *Homo ergaster* is a juvenile specimen. Nevertheless, it has been compared here with adult mean shapes. This should not pose a problem since (as shown in Chapter III, inter-specific size and shape variation, pp. 264 and 267-268) *patterns* of size variation can be expected to be similar for juvenile as well as adult specimens. *A. afarensis* was not included in any of these comparisons since its sample consists of only one lumbar vertebra. In great apes, Th12 (Asian apes) and Th13 (African apes) were included to bring the total number of vertebrae to five.

5.4. Results

5.4.1. Analysis 1, intra and inter-specific differences in vertebral size

In a first step, differences in vertebral size between fossil taxa and between fossil taxa and modern hominoids are assessed. Thus in this analysis, the vertebral centroid sizes of the fossil specimens are tabulated (presented in table 5.2) and compared to the mean vertebral centroid sizes and 95% confidence limits of modern hominoid taxa. A comparison of fossil centroid sizes with those of modern taxa is conducted level by level.

From table 5.2 it can be seen that the single lumbar vertebra representing *A. afarensis* (possibly an L3) fits within the 95% confidence limits of both *Pongo* sexes. All other modern taxa have larger L3 vertebrae when compared to the *A. afarensis* specimens. Compared to the other fossil vertebrae in table 5.2, the size of the *A. afarensis* vertebra is closest to the *A. africanus* specimen Sts14.

The specimens of *A. africanus* fall into two categories: Sts14 has the smallest lumbar vertebrae in the comparison. Its vertebral centroid sizes regularly fall outside of the 95%

confidence limits of all modern taxa at all comparison levels with the exception of L2. Here, the Sts14 vertebra barely fits within the minimum of the 95% confidence limit of female *Pongo* (modern taxa with smallest lumbar vertebrae). In addition, Sts14 is the smallest fossil specimen. In contrast, the lumbar vertebrae of *A. africanus* Stw431 are very different in size from those of *A. africanus* Sts14. L1 and L2 fall well within the 95% confidence limits of *Pongo* and *Pan* females. L3 additionally fits well within the 95% limits of male *Pan*, whereas L4 and L5 both lie within the 95% confidence interval of *Pan*, *Pongo*, and female *Gorilla*. However, *A. africanus* Stw431 L5 falls outside the 95% confidence limits of human L5 and male *Gorilla* L4. The two single lumbar vertebrae of *A. africanus* specimens Stw8 (possibly L2) and Stw572 (possibly L4) both fit well within the 95% confidence intervals of female *Pan* and *Pongo* at their respective comparison levels. They are both smaller than *A. africanus* Stw431 but also clearly bigger than the *A. africanus* specimen Sts14.

Taxon	L1	L2	L3	L4	L5
Gorilla gorilla ♂	**9.3688** ± 1.1328 (1sd = 0.5664)	**9.2323** ± 1.5442 (1sd = 0.7721)	**9.2997** ± 0.9836 (1sd = 0.4918)	**8.8452** ± 1.0204 (1sd = 0.5102)	
Gorilla gorilla ♀	**7.6454** ± 0.8672 (1sd = 0.4336)	**7.6523** ± 0.8134 (1sd = 0.4067)	**7.5803** ± 0.9276 (1sd = 0.4638)	**7.2023** ± 0.6836 (1sd = 0.3418)	
Pan troglodytes ♂	**6.8021** ± 0.6266 (1sd = 0.3133)	**7.1760** ± 0.6820 (1sd = 0.341)	**7.0925** ± 0.6026 (1sd = 0.3013)	**6.7620** ± 0.4886 (1sd = 0.2443)	
Pan troglodytes ♀	**6.5234** ± 0.6252 (1sd = 0.3126)	**6.7448** ± 0.5614 (1sd = 0.2807)	**6.7427** ± 0.270 (1sd = 0.1350)	**6.5495** ± 0.8864 (1sd = 0.4432)	
Pongo pygmaeus ♂	**7.4098** ± 0.5798 (1sd = 0.2899)	**7.5786** ± 0.5468 (1sd = 0.2734)	**7.4614** ± 1.4266 (1sd = 0.7133)	**7.4670** ± 0.7958 (1sd = 0.3979)	
Pongo pygmaeus ♀	**6.2578** ± 0.3758 (1sd = 0.1876)	**6.3010** ± 0.6238 (1sd = 0.3119)	**6.3510** ± 0.688 (1sd = 0.3440)	**6.2278** ± 0.284 (1sd = 0.1420)	
Homo sapiens ♂	**7.9714** ± 0.8966 (1sd = 0.4483)	**8.3378** ± 0.8614 (1sd = 0.4307)	**8.6042** ± 0.959 (1sd = 0.4795)	**8.7382** ± 0.546 (1sd = 0.2730)	**9.0939** ± 1.0134 (1sd = 0.5067)
Homo sapiens ♀	**7.3488** ± 0.8272 (1sd = 0.4136)	**7.6983** ± 0.7726 (1sd = 0.3863)	**7.9049** ± 0.7662 (1sd = 0.3831)	**7.9633** ± 0.786 (1sd = 0.3930)	**8.3327** ± 0.8578 (1sd = 0.4289)
A. afarensis AL288-1			**6.072**		
A. africanus Sts14	**5.426**	**5.702**	**5.543**	**5.527**	**6.006**
A. africanus Stw431	**6.326**	**6.825**	**6.716**	**7.174**	**6.972**
A. africanus Stw572				**6.512**	
A. africanus Stw8		**6.461**			
Homo ergaster KNM-WT 15000	**6.465**		**6.840**	**7.495**	**7.382**

Table 5.2 Tabulation of vertebral centroid sizes, fossil and modern taxa. Modern taxa: mean sizes ± 2 sds (= proxy for 95% of variation)

Table 5.2 also shows that the juvenile *Homo ergaster* specimen has the largest lumbar vertebrae when compared to the other fossil taxa. At each comparison level, where there is a *Homo ergaster* vertebra available, they all surpass the largest *A. africanus* specimen Stw431 in centroid size. At each comparison level, the vertebral centroid size of *Homo ergaster* fits comfortably within the 95% confidence limits of *Pongo* and *Pan* (both sexes) and male *Gorilla*. From L3 to L5 they also fit within the 95% confidence limits of female *Gorilla*. The *Homo ergaster* L4 vertebra even fits within the low end of the *Homo sapiens* female 95% confidence limit. The last lumbar of *Homo ergaster*, however, falls outside the 95% confidence limit of modern humans (both sexes) but is well within the borders of the 95% confidence limit of *Pongo*, *Pan*, and female *Gorilla*.

Thus, results from comparing fossil vertebral centroid size with those of modern taxa indicate that the *A. afarensis* specimen AL-288-1 shows vertebrae similar in size to female *Pongo*. Taking into consideration the juvenile status of the *Homo ergaster* specimen, one might infer that its adult vertebral size would have reached adult *Homo sapiens* (and *Gorilla*) dimensions (see later analyses of juveniles). *A. africanus* on the other hand, seems to have lumbar vertebrae similar in size to *Pan* and *Pongo* (both sexes). At least this is the case for specimens Stw8, 431, and 572. *A. africanus* Sts14 on the other hand has the smallest lumbar vertebrae in the entire sample.

On visual inspection, and also indicated by the compilation of vertebral centroid sizes in table 5.2, the vertebrae of *A. africanus* specimens Stw431, Stw572, and Stw8 differ considerably in size from the *A. africanus* specimen Sts14. To clarify if these differences in vertebral size express potential sexual dimorphism in *A. africanus*, the results from Chapter III (intra-specific differences in vertebral size and shape from p. 153.) assessing sexual dimorphism in vertebral centroid size and various comparison levels are reproduced in table 5.3. Size differences in vertebral centroid size between *A. africanus* Sts14 (presumably a female) and either centroid size of Stw431 or the mean centroid size calculated from those of Stw431 and Stw8 or Stw572 (depending on the comparison level) are displayed together with the results for modern taxa in table 5.3. No significance level has been calculated for the fossil taxon since the comparison consists of only two specimens. However, the ratio of vertebral sizes between sexes size observed within *A. africanus* (Sts14 vs. the other *A. africanus* specimens) is larger than the ratio of mean centroid sizes observed between the sexes of *Homo sapiens* and *Pan* and smaller than those of *Gorilla* and *Pongo*. However, *A. africanus* resembles modern

humans in so far that here too, a relatively small ♂/♀ weight ratio is paired with sexual dimorphism in vertebral centroid size larger than that observed in *Pan*.

Species	L1	L2	L3	L4	L5	♂/♀ weight ratio
Homo sapiens Males vs. females	**0.6226 p=0.001**	**0.6337 p=0.001**	**0.6993 p=0.001**	**0.7786 p=0.001**	**0.7612 p=0.001**	**1.2**
Gorilla gorilla Males vs. females	**1.7233 p=0.001**	**1.5882 p=0.001**	**1.7194 p=0.001**	**1.6429 p=0.001**		**1.95**
Pan troglodytes Males vs. females	**0.3380 p=0.003**	**0.4312 p=0.001**	**0.3574 p=0.002**	0.2125 p=0.115		**1.3**
Pongo pygmaeus Males vs. females	**1.115 p=0.001**	**1.3833 p=0.001**	**1.267 p=0.001**	**1.239 p=0.001**		**2.0**
A. africanus Stw8, 431, and 572 vs. Sts14	**0.900**	**0.941**	**1.173**	**1.316**	**0.966**	**1.3**

Table 5.3 Assessment of vertebral size and body weight differences and ratios between *A. africanus* specimens in comparison to sexual dimorphism in vertebral size and body weight observed in modern hominoid taxa. Modern taxa: line 1: mean difference and ratios in centroid size between sexes (in cm), line 2: level of significance, tested with independent t-test, $p<0.001$. All significant differences remain so after Bonferroni correction (significance tests n = 16, familywise error = 56.0%, p-Bonferroni corrected = 0.003)

5.4.2. Analysis 2, intra and inter-specific differences in vertebral shape

The aim of analysis 2 is to assess differences in vertebral shape between fossil and modern taxa and between the fossils. The choice of analysis is first to carry out GPA/PCA of single vertebrae (at various comparison levels) of whole samples to get an overview of the relations of the fossil shapes to the scatters of shape variation of each other and in relation to modern taxa. The next step is to compute species mean shapes at various comparison levels and to compare these with each other and the fossils in order to better assess differences in a more easily interpreted lower dimensional space.

Australopithecine taxa

First, GPA/PCA was performed on the data of all australopithecine specimens. Figure 5.1 shows a scatter plot of PC1 versus PC2 of all australopithecine lumbar vertebrae. PC1 separates different vertebral levels (L1, L2,...) from each other; L1 is positioned on the left half of the axis of PC1, whereas L5 is on the right half of the axis of PC1 (see figure 5.1). PC2 separates the various specimens along its axis. The consecutive vertebrae of specimens Sts14 and Stw431 are joined by dotted lines for easier reading.

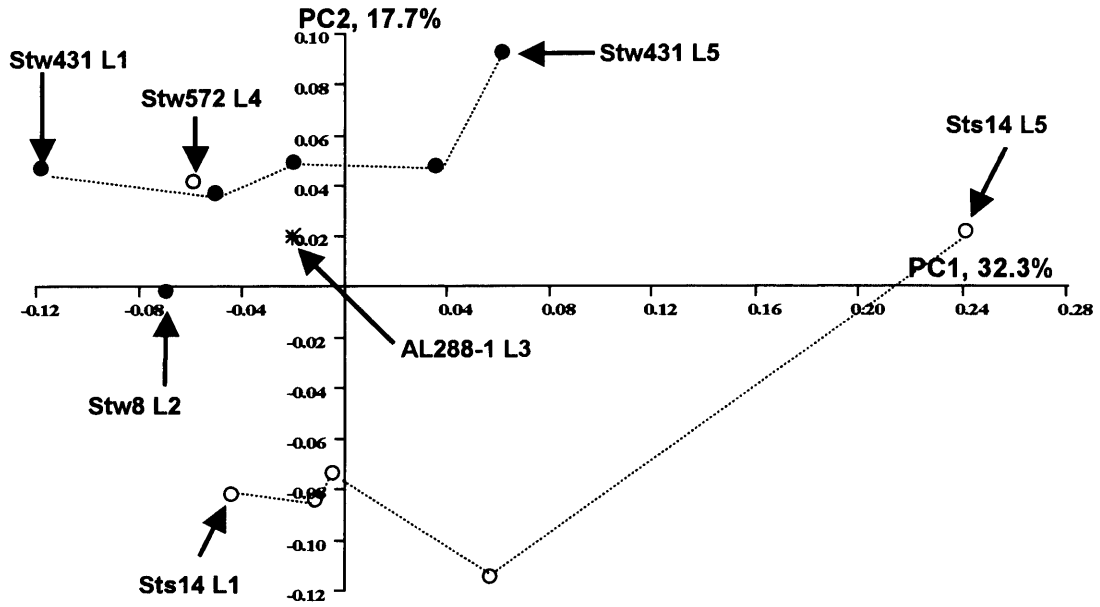
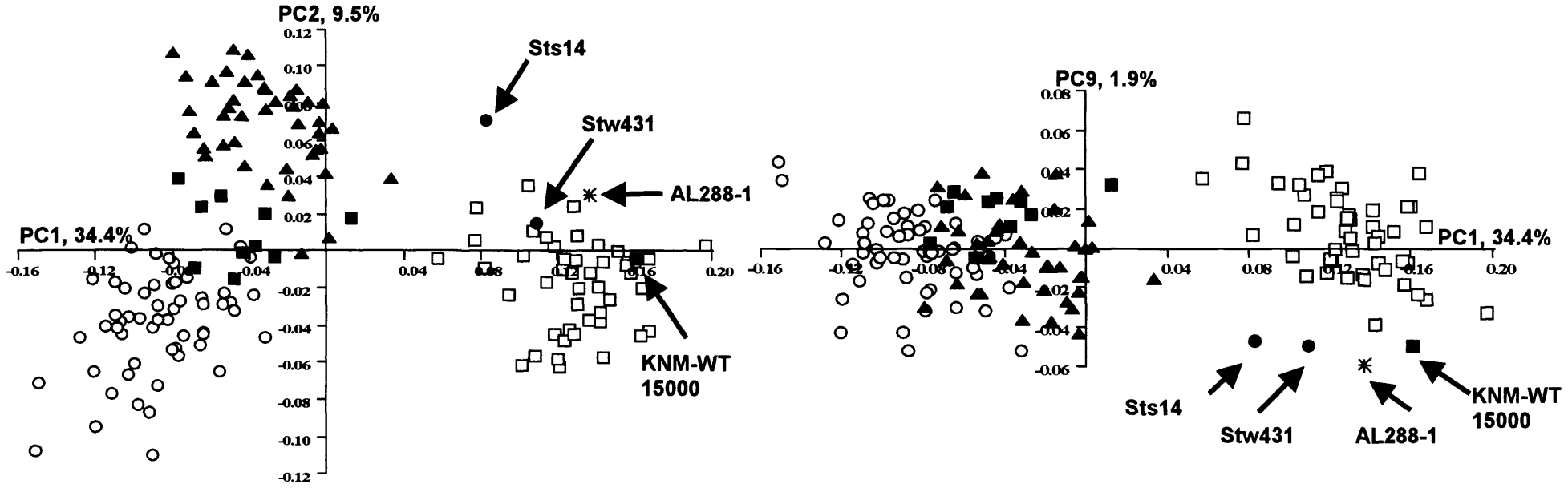


Figure 5.1 Scatter plot of PC1 vs. PC2, all *Australopithecus* vertebrae. Consecutive vertebrae of specimens Sts14 and Stw431 are joined by dotted lines. ○ = *A. africanus* Sts14, ● = *A. africanus* Stw431, ○ = *A. africanus* Stw572 ● =, *A. africanus* Stw8, * = *A. afarensis* AL288-1

The australopithecine specimens all cluster closely relative to the differences in shape between vertebral levels. Sts14 is distinguished from the others on PC2 and its last lumbar vertebra on PC1. Importantly, *A. afarensis* does not appear very different in shape from the *A. africanus* specimens. Only PC5 (6.5% TSV) discriminates between *A. afarensis* and *A. africanus* yet the separation is weak. The main difference between the two taxa consists of differences in relative length of the costal processes. Since these are not preserved in *A. afarensis* and had to be reconstructed this is not a reliable result. Furthermore, differences in shape between *A. afarensis* and *A. africanus* summarized by PC5 are seen in the vertebral body - it is relatively longer in *A. afarensis* - and the spinous process is relatively shorter in *A. afarensis.*



A: PC1 vs. PC2, level 2

B: PC1 vs. PC9, level 2

Figure 5.2. Scatter plots of PC1 vs. PC2 **(A)** and PC1 vs. PC9 **(B)** extracted from full samples of adult modern hominoids and all fossil taxa at comparison **level 2**. Arrows indicate specific fossil specimens ○= *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*, □ = *Homo sapiens*, ■ = *Homo ergaster*, ● =, *A. africanus*, *= *A. afarensis*

5.4.3 Comparison of single vertebral shapes at various comparison levels between modern hominoids and fossil hominin taxa

This analysis consists of GPA/PCA of the shape data of full adult samples of modern hominoid taxa and the fossil hominins at each vertebral comparison level. To facilitate the presentation of results, only those stemming from the comparison of all taxa at comparison level 2 are presented and described in full here. This is because at this comparison level, the largest number of different taxa (including *A. afarensis*) is present. Scatter plots of PCs extracted from GPA/PCA and results for the other four comparison levels (levels 1, solution 1, 1, solution 2, 3, and 4) are also presented but are only described if they differ considerably from comparison level 2. This section is followed by a separate comparison of the *Homo ergaster* lumbar vertebrae with immature specimens of modern taxa.

Comparison level 2

At comparison level 2, the third lumbar vertebra of modern humans and fossil taxa (*Homo ergaster, A. afarensis*, and *A. africanus*) is compared with the second lumbar vertebra of the great apes. Differences in overall lumbar vertebral shape are largest between modern humans plus all fossil taxa, and the great apes. Differences in shape between these two groups are summarized by PC1 (34.4%).

Figure 5.2 shows two scatter plots of PC1 versus PC2 and PC9 respectively. PC1 and 2 are the two most powerful PCs identified by discriminant analysis in separating the taxa. Modern humans and the various fossil hominins are clearly separated from all great ape taxa along the axis of PC1. In addition, on this PC a weak separation of between *Gorilla* and *Pongo*, and *Pan* is detected (see figure 5.2 A and B). PC2 on the other hand, best separates *Gorilla* from both *Pongo* and *Pan* (figure 5.2A). PC2 also – to some degree – sets *A. africanus* Sts14 apart from the human sample as well as the other *A. africanus* specimen and *A. afarensis*. The other *A. africanus* specimen Stw431 is positioned within the human sample distribution as is the *Homo ergaster* specimen. *A. afarensis* lies close to the border of the human sample distribution along the axis of PC1. PC3 separates *Pongo* from all other great apes (plot not shown). PC 9 best discriminates between all fossil taxa and the modern human sample (figure 5.2B). PC9 is of a relatively low order and summarizes only 1.9% of the total shape variation observed in the total sample. The *A. afarensis* 288-1 specimen is now farthest removed from the modern human sample without being close to the great ape samples. The

differences in shape summarized along PC9 are predominantly found in the length and orientation of vertebral processes: the fossil taxa have relatively longer costal and superior articular processes than those of modern humans. In contrast, their inferior articular processes are relatively shorter. The spinous process is more cranially orientated compared to the relatively horizontally protruding human spinous process. These differences in shape will be discussed later on in the present chapter. In the following section, a summary of the other four comparison levels is presented.

5.4.4 Summary of remaining comparison levels

Comparison level 1, solution 1

At comparison level 1, solutions 1, the first lumbar vertebrae of all taxa are compared with each other. The sample contains two *A. africanus* (Sts14, Stw431) and the *Homo ergaster* specimen. As at comparison level 2, PC1 (34.5%) summarizes differences in shape between humans, *A. africanus*, and the great apes. PC2 (9.6%), on the other hand, separates small apes (*Pan*) from large apes (*Gorilla* and *Pongo*) (see figure 5.3).

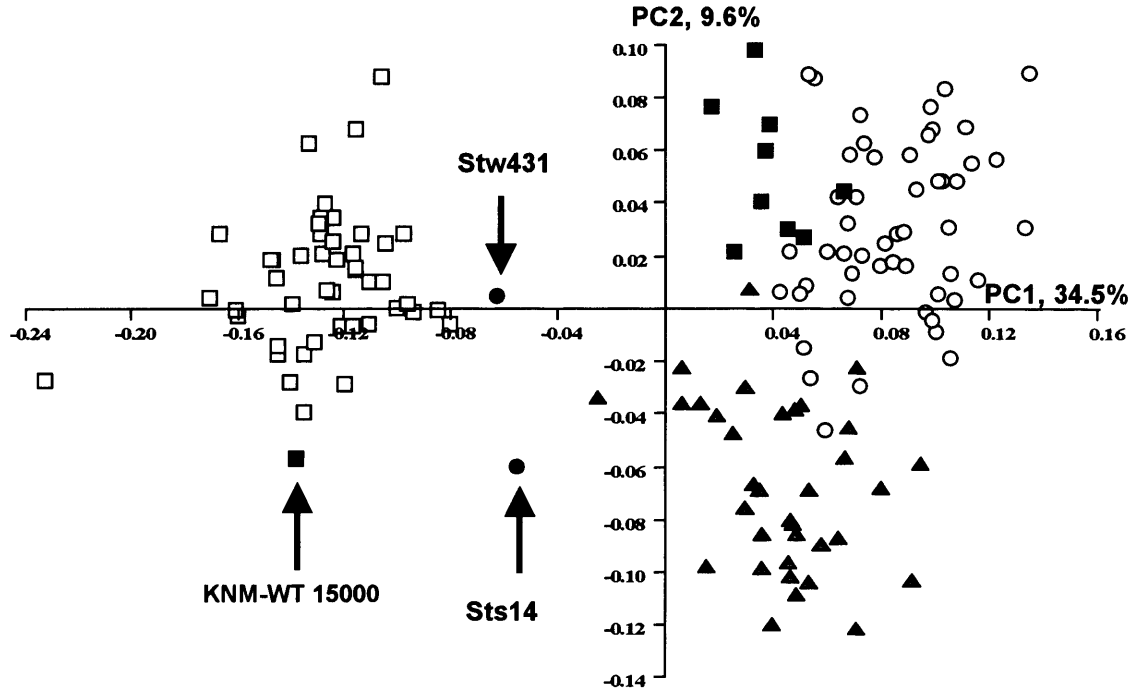


Figure 5.3 Scatter plot of PC1 vs. PC2 extracted from full samples of adult modern hominoids and all fossil taxa at comparison **level 1, solution 1**. Arrows indicate specific fossil specimens. ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*, □ = *Homo sapiens*, ■ = *Homo ergaster*, ● = *A. africanus*

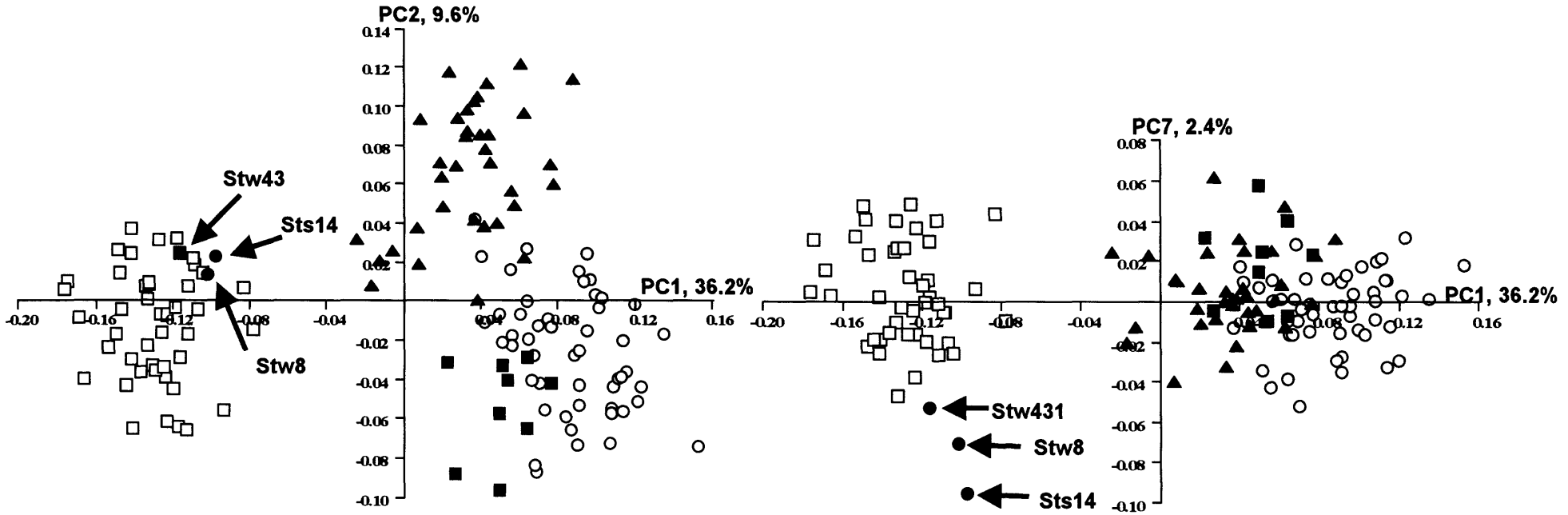
Additionally, *A. africanus* Sts14 and *Homo ergaster* are separated from the human sample distribution along the axis of PC2, whereas *A. africanus* Stw431 is not separated from the human sample. None of the other PCs was identified to be successful in separating fossil hominins from the human sample distribution.

Comparison level 1, solution 2

At this comparison level, the second lumbar vertebra of modern humans and *A. africanus* were compared with L1 of all modern great apes. *A. africanus* is represented by the specimens Sts14, Stw431, and Stw8. No *Homo ergaster* vertebra was included because the second lumbar vertebra of the one available specimen is too fragmentary to be reconstructed for measurements. Scatter plots of PCs 1 versus PC2 and PC1 versus PC7 are presented in figure 5.4. As at all comparison levels, PC1 (36.2%), separates *Homo sapiens* from all great ape taxa. However, at this comparison level, it failed to separate *A. africanus* from *Homo sapiens* along its axis (see figure 5.4A). The next most powerful PC (PC2, 9.6%) separates small apes (*Pan*) from large apes (*Gorilla* and *Pongo*). Again, PC3 (5.2%) separates African and Asian apes. The relatively weak PC7 (2.4%) best separates *A. africanus* from both *Homo sapiens* and the great ape samples along its axis (figure 5.4B).

Comparison level 3

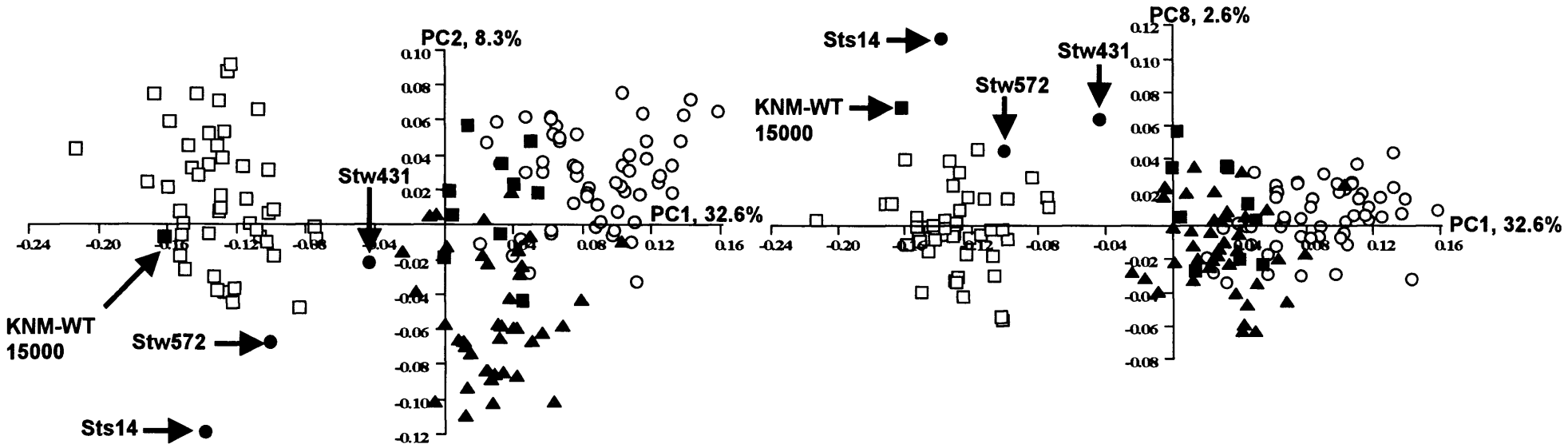
At comparison level 3, the fourth lumbar vertebrae of humans, *Homo ergaster*, and *A. africanus* are compared with the third (second last) lumbar of the modern great apes. *A. africanus* is represented by three lumbars belonging to specimens Sts14, Stw431, and Stw572. Along the axis of PC1 (32.6%), humans, *Homo ergaster*, and the *A. africanus* specimen Stw572 are separated from the *A. africanus* specimen Stw431, and all great apes (see figure 5.5A). PC1 also separates the sample of *Gorilla* from *Pongo* and *Pan*. PC2 (8.3%), on the other hand, discriminates between large (*Gorilla* and *Pongo*) and small apes (*Pan*). Along the axis of PC2, the *A. africanus* specimen Stw431 is clearly separated from the two other *A. africanus* specimens (figure 5.5A). PC8 (2.6%) is the strongest discriminator between modern and fossil taxa (see figure 5.5B).



A: PC1 vs. PC2, level 1, solution 2

B: PC1 vs. PC9, level 1, solution 2

Figure 5.4 Scatter plots of PC1 vs. PC2 **(A)** and PC1 vs. PC7 **(B)** extracted from full samples of adult modern hominoids and all fossil taxa at comparison **level 1, solution 2**. Arrows indicate specific fossil specimens. ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*



A: PC1 vs. PC2, level 3

B: PC1 vs. PC6, level 3

Figure 5.5 Scatter plots of PC1 vs. PC2 **(A)** and PC1 vs. PC8 **(B)** extracted from full samples of adult modern hominoids and all fossil taxa at comparison **level 3**. Arrows indicate specific fossil specimens. ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*, □ = *Homo sapiens*, ■ = *Homo ergaster*, ● = *A. africanus*

Comparison level 4

At comparison level 4, the last lumbar vertebrae of all taxa were compared with each other. *A. africanus* is represented by the specimens Sts14 and Stw431. There was a vertebra available for *Homo ergaster*. PC1 (43.2%) again best separates humans and the fossil taxa from all great apes along its axis (see figure 5.6). *A. africanus* Sts14 and the *Homo ergaster* specimen lie well within the human sample variation along the axis of PC1. *A. africanus* Stw431 hovers at the borders of the human data variation as it did at other comparison levels. PC2 (6.0%) summarizes differences in shape between Asian and African apes. The most powerful taxon discriminators (apart from PC1) PCs 4 and 5, best discriminate between fossil taxa and modern humans. In this, PC4 (4.0%) best discriminates the *A. africanus* specimen Stw431 from the human data distribution whereas PC5 (3.5%) does the same for Sts14.

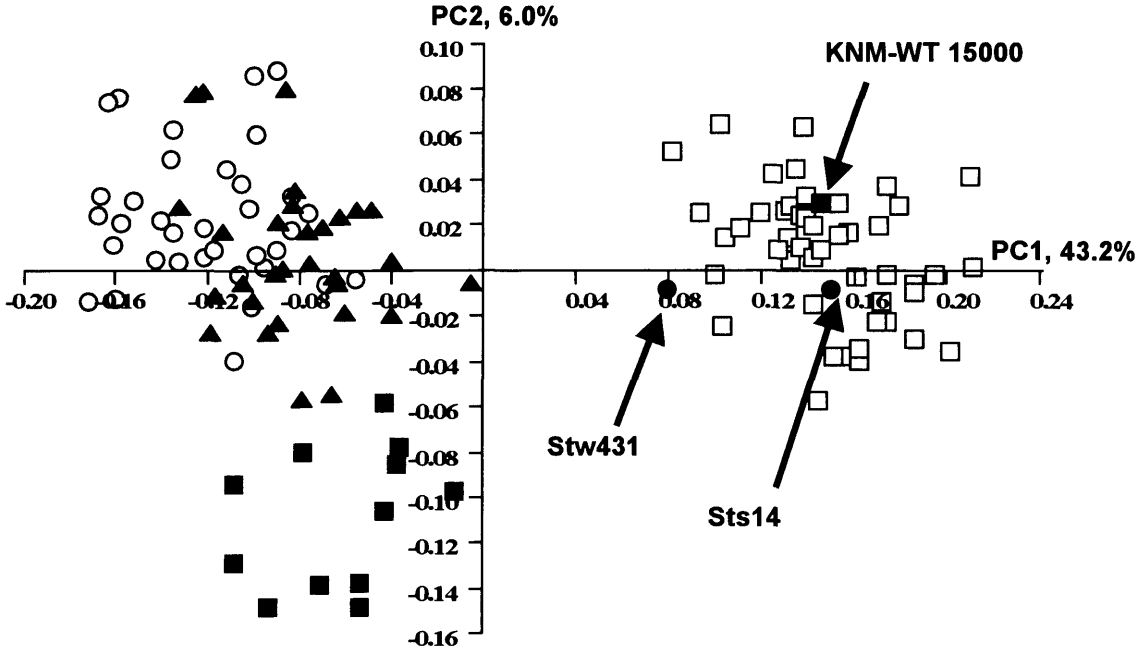


Figure 5.6 Scatter plot of PC1 vs. PC2, comparison level 4. Arrows indicate specific fossil hominin specimens. ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ■ = *Pongo pygmaeus*, □ = *Homo sapiens*, ■ = *Homo ergaster*, ● = *A. africanus*

5.4.5 Comparison of immature modern specimens with *Homo ergaster*

In the previous comparisons, the *Homo ergaster* specimen usually clusters closely with the adult modern human sample and has no overlap with any of the great ape taxa. However, since this is a juvenile specimen, differences between humans and *Homo*

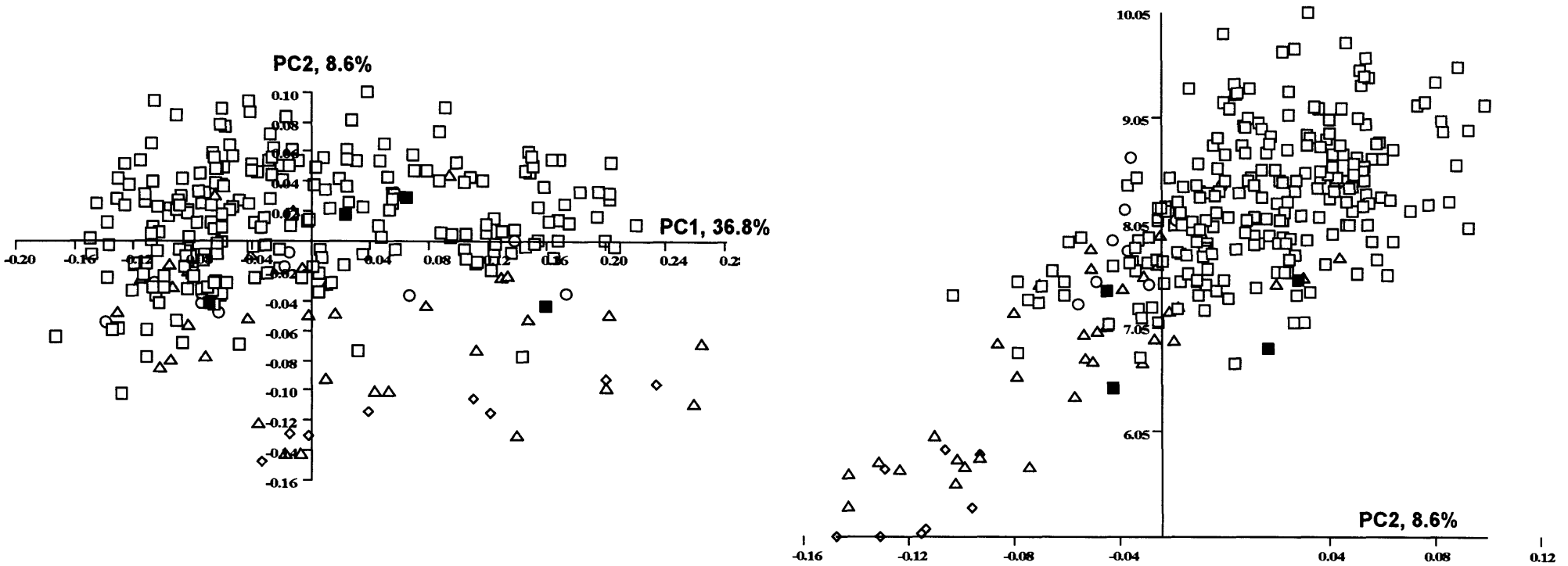
ergaster might be due to differences in maturation. Therefore, it is compared below to samples of each modern taxon, containing adult, sub-adult, juvenile, and infant specimens.

Comparison of full *Homo sapiens* sample with *Homo ergaster*

The shape variation between and among the full *Homo sapiens* sample and the four *Homo ergaster* vertebrae was explored with GPA/PCA. Figure 5.7A shows a scatter plot of PC1 vs. PC2. The *Homo ergaster* vertebrae all lay within the range of human vertebral shape variation (see figure 5.7A). None of the PCs was able to separate all the *Homo ergaster* vertebrae from the human data distribution. PC1 (36.8%) discriminates between the different lumbar vertebrae (L1, L2, etc). PC2 (8.6%) separates different age groups along its axis (infant, juveniles etc). Additionally, a plot of PC2 (age group discriminator) versus centroid size reveals that the *Homo ergaster* vertebrae fall within the distribution of the older (around 17 years of age) human juvenile specimens (see figure 5.7B), and some of the smaller adult humans. The age of the human juvenile specimens ranges from age 7 (youngest) to age 17.7 (oldest); the human specimens classed as infant in this analysis are 4 and 4.5 years old respectively (Humphrey, 1998).

Comparison of full great ape samples with *Homo ergaster*

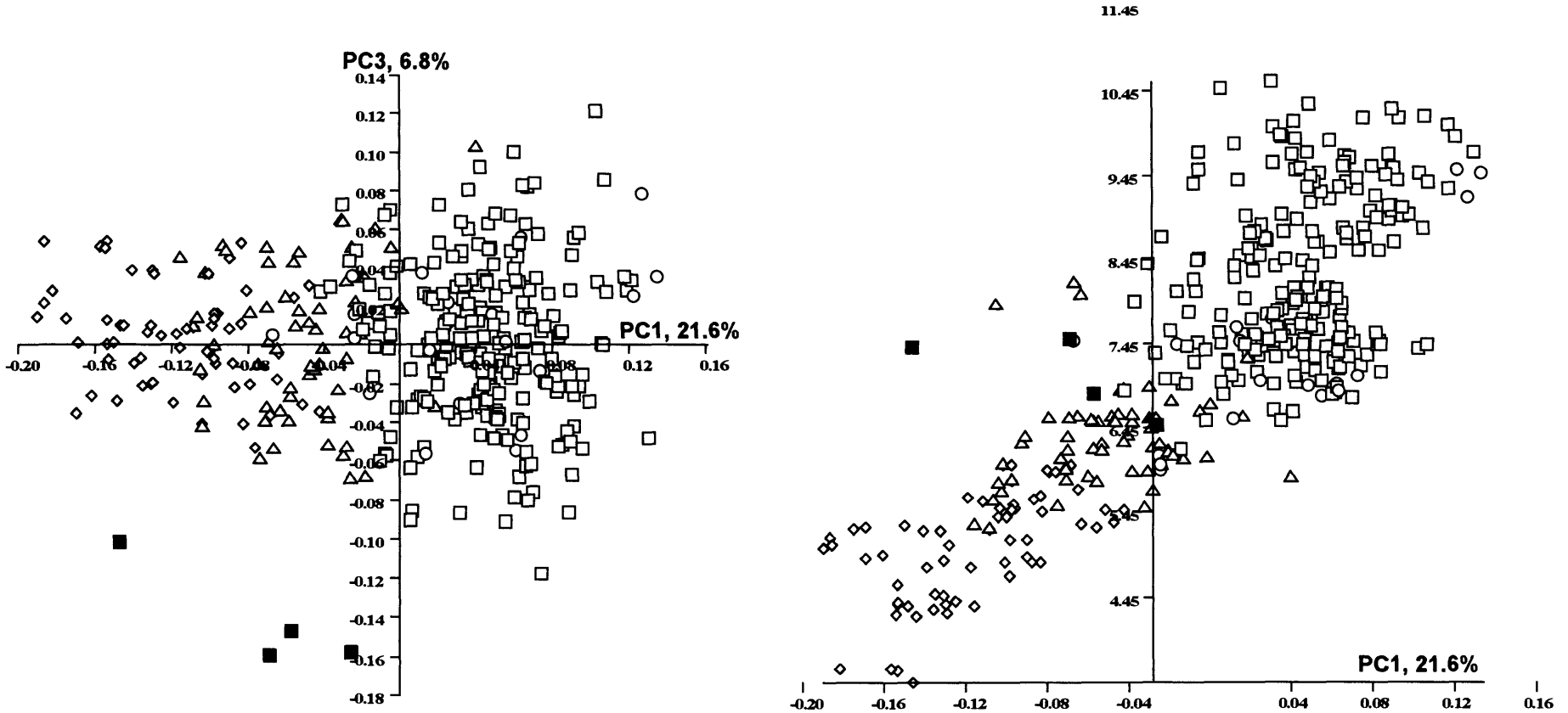
As might be expected given the foregoing results, GPA/PCA of full great ape samples and *Homo ergaster* the latter is distinctive. In all three great ape comparisons, PC1 best discriminates between age groups (see figures 5.8A, 5.9A, and 5.10A). In analyses with African apes PC2 separates different vertebrae along its axis. In the analysis with *Pongo* PC2 separates *Homo ergaster* (figure 5.10A) and PC3 discriminates the different lumbar vertebrae. In the analyses with African apes, PCs 4 and 5 are the strongest discriminators between *Homo ergaster* and *Pan* and *Gorilla*. Thus, as expected from previous results (see analysis 2), *Homo ergaster* is different in vertebral shape from all modern great apes (see figures 5.8A, 5.9A, and 5.10A). Scatter plots of PC1 (discriminator between age groups) versus centroid size show that *Homo ergaster* falls well within the range of *Gorilla* (figure 5.8B) but is distinct from both *Pan* and *Pongo* (figure 5.9B and 5.10B). Within the *Gorilla* distribution, *Homo ergaster* is closest to the older juvenile specimens (great ape juveniles are 5 to 7 years old) (Bösch and Bösch-Achermann, 2000; Dean, 2000; Holly Smith et al., 1994; Nishida et al., 1990; Zihlman et al., 2004). In the comparisons with *Pan* and *Pongo*, *Homo ergaster* lies closest elder juveniles and small adult specimens.



A: PC1 vs. PC2, full sample

B: PC1 vs. centroid size

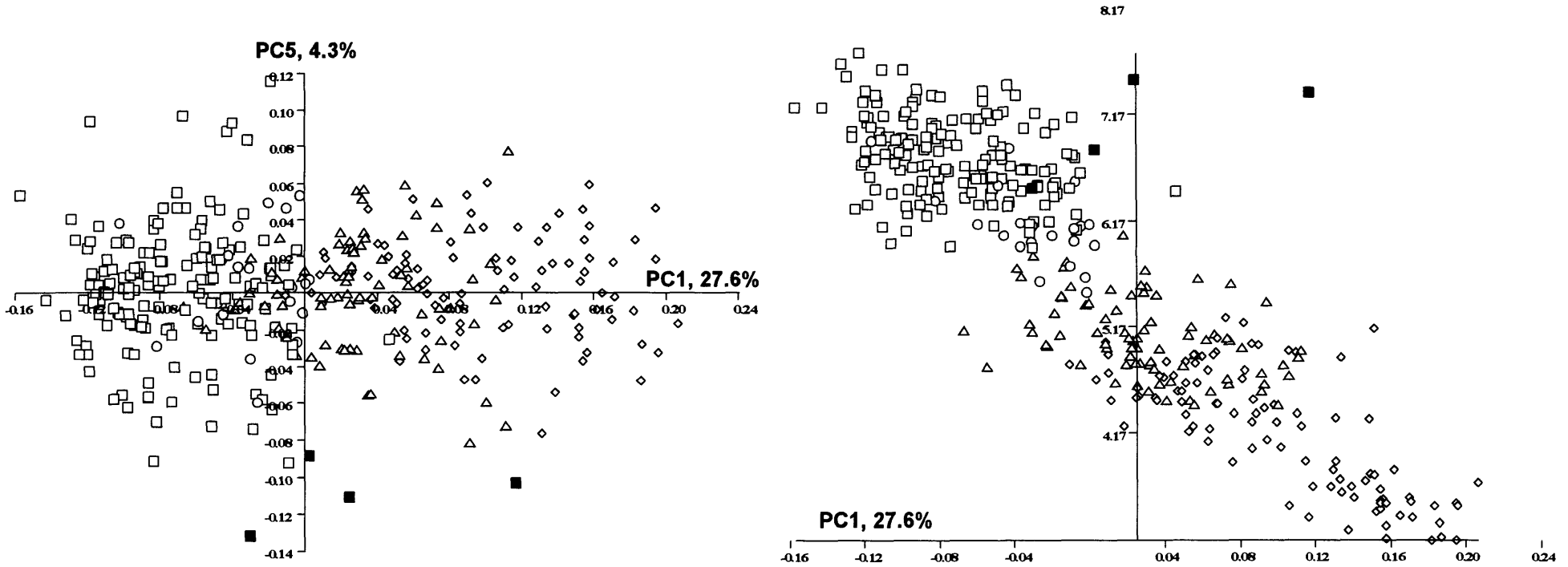
Figure 5.7 Scatter plots of PC1 vs. PC2 **(A)** and PC2 vs. centroid size **(B)**, full human sample and *Homo ergaster*. Juvenile and infant specimens are highlighted in grey. *Homo sapiens*: □ = adults, ○ = sub-adults, △ = juveniles, ◇ = infants, ■ = *Homo ergaster*



A: PC1 vs. PC3, full sample

B: PC1 vs. centroid size

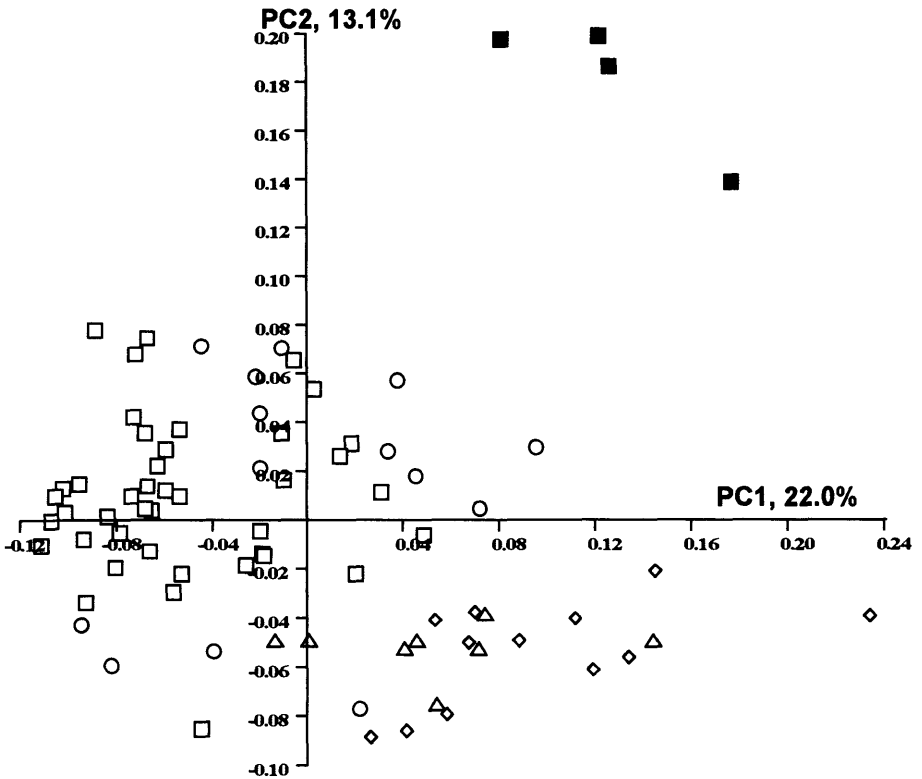
Figure 5.8 Scatter plots of PC1 vs. PC3 **(A)** and PC1 vs. centroid size **(B)**, full *Gorilla* sample and *Homo ergaster*. Juvenile and infant specimens are highlighted in grey. *Gorilla*: □ = adults, ○ = sub-adults, △ = juveniles, ◇ = infants, ■ = *Homo ergaster*



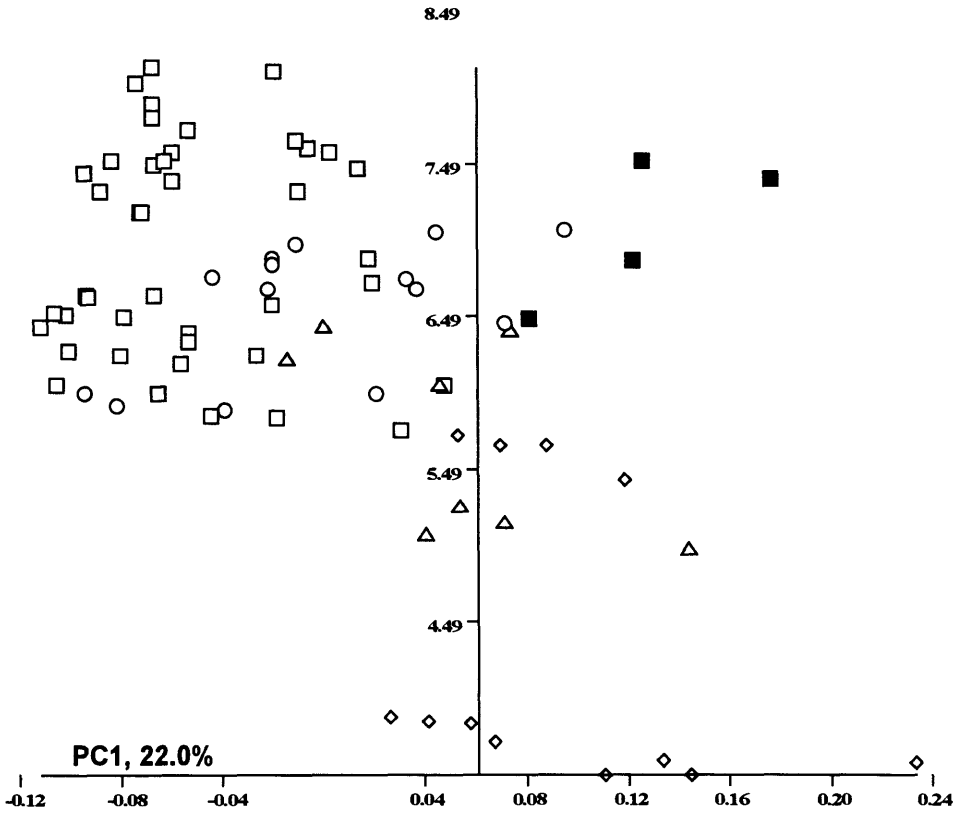
A: PC1 vs. PC5, full sample

B: PC1 vs. centroid size

Figure 5.9 Scatter plots of PC1 vs. PC5 **(A)** and PC1 vs. centroid size **(B)**, full *Pan* sample and *Homo ergaster*. Juvenile and infant specimens are highlighted in grey. *Gorilla*: □ = adults, ○ = sub-adults, △ = juveniles, ◇ = infants, ■ = *Homo ergaster*



A: PC1 vs. PC2, full sample



B: PC1 vs. centroid size

Figure 5.10 Scatter plots of PC1 vs. PC2 **(A)** and PC1 vs. centroid size **(B)**, full *Pongo* sample and *Homo ergaster*. Juvenile and infant specimens are highlighted in grey. *Pongo*: □ = adults, ○ = sub-adults, △ = juveniles, ◇ =infants, ■ = *Homo ergaster*

5.4.6 Summary

Comparison of adult samples

Results from the comparison of large samples of recent hominoids with the available fossil hominin lumbar vertebrae at various comparison levels reveal that the largest differences in vertebral shape are to be observed between humans and all fossil hominins, and the great ape taxa (shape differences usually summarized by PC1). At none of the comparison levels did any of the fossil hominins overlap with the great ape shape variation. On the other hand, at some of the comparison levels, there is some overlap between the fossil hominins and modern humans. In general, *Homo ergaster* showed the largest overlap with the modern human data distribution and often lies within the limits of human shape variation. Specimens belonging to *A. africanus* usually lie at closest to but beyond the human distribution. Of the two *A. africanus* specimens Stw431 and Sts14, Stw431 often lies closer to the human sample distribution than Sts14. Nevertheless, in all comparison, Stw431 usually lies closer of all fossils to the African ape sample distributions, whereas Sts14 usually farther away – especially at the levels of the second last and last lumbar vertebrae.

Consistent with differences in sample size, PCs which discriminate between the modern great ape taxa are usually of higher order (PCs 2, 3) and summarize larger percentages (approximately 5 to 10%) of the total shape variation than those PCs which summarize differences in shape discriminating between modern humans and the fossil taxa. These PCs are usually of smaller order (PC 7, 8, and 9) and summarize approximately 1.5 to 2.5% of the total shape variation with the exception of comparison level 4 (last lumbars). At this comparison level, differences in shape between humans and great apes are larger (indicated by the larger percentage of total shape variance summarized by PC1 at this comparison level) and PCs which most successfully discriminate between human and fossil taxa are of somewhat higher order (PCs 4 and 5). This indicates the possibility of larger differences in vertebral shape at level 4 than at previous comparison levels. Differences in shape between humans and fossil taxa are usually smaller than those between humans and great apes, between fossil hominins and great apes, and between all great apes.

***Homo ergaster* compared to modern taxa**

The results from this comparison show very little difference in vertebral size and shape between humans and *Homo ergaster* especially when the subadult status of this fossil is taken into account. Between *Gorilla* and *Homo ergaster*, there is a good match between *Gorilla* juveniles and *Homo ergaster* in relation to vertebral size. However, the differences in shape are substantial. Between *Pongo* and *Pan*, and *Homo ergaster* there are large differences observed in both vertebral size and shape.

5.4.7 Analysis 3, exploring inter-specific differences in species mean shapes

In analysis 2, whole samples of each taxon were explored at various comparison levels. The resulting shape space is high dimensional and differences between fossils and between fossils and extant taxa are to some extent obscured by differences between individuals within and between each taxon. In order to reduce dimensionality and to be able to directly compare differences in shape between species means, further analyses were carried out. The first analysis comprised the examination of inter-specific differences in mean shape between modern and fossil taxa. To visualize differences in vertebral shape between the taxa (position of the taxa in relation to each other), three-dimensional scatter plots of the species means were produced and the direction and distance from the centroid (calculated from all species means in the analysis) was indicated by spikes.

Mean *A. africanus* lumbar vertebral shape compared with modern hominoid means

In a first step, the species mean shapes of all modern taxa were compared with the mean *A. africanus* lumbar vertebral shape. Figure 5.11 shows two different views of a three dimensional scatter plot of PC 1 versus PC2, versus PC3 from the GPA/PCA analysis of these mean shapes. The first three PCs summarize 95.1% of the total shape variation. The plots show PC1 discriminating strongly between mean *Gorilla* and *A. africanus*. PC2 on the other hand, separates humans and *A. africanus* from *Pongo*, and PC3, discriminates between *A. africanus* and humans. That *A. africanus* is so distinct from extant taxa including *Homo* is of interest – the two-dimensional scatter plots from analysis 3 (full sample analysis) did not indicate this. In part this should be read with caution since population scatters are not shown but in part this reflects the advantage of working with reduced spaces (i.e., low dimensionality by using means) in removing the

swamping effect of large modern samples to examine the relations of small numbers of fossils.

A. afarensis lumbar vertebral shape compared with modern hominoid means

Since the sample of *A. afarensis* consists of only 1 lumbar vertebra (highly likely L3), this vertebra is compared to the species means at comparison level 2. Figure 5.12 shows two different views of a three-dimensional scatter plot of PC1 versus PC2 versus PC3 of the GPA/PCA analysis of these mean shapes. The three PCs summarize 94.1% of the total shape variation. The relations of taxa are very similar to that previously observed between modern taxa and *A. africanus*. PC 1 discriminates between *Gorilla* and *A. afarensis*. PC2 separates *Homo* from *Pongo* and PC3 summarizes differences in shape between humans and *A. afarensis*.

Australopithecine taxa compared with modern hominoid means

The previous two comparisons separately compared each australopithecine taxon with modern hominoid taxa. In both cases, the positions of the mean vertebral shapes of the fossil taxa are closest to modern humans. However, at the same time, they are rather different from all modern hominoid taxa and occupy positions somewhat removed from that of modern humans. Thus, in the present comparison, both australopithecine taxa are compared simultaneously with the modern taxa. To facilitate comparisons, mean shapes were calculated for all taxa at comparison level 2 (L3 modern humans and fossil taxa, L2 all great apes), with the exception of *A. afarensis* since that sample consisted of only one vertebra. Figure 5.13 shows two views of the scatter plot of PC1 versus PC2 versus PC3 of the GPA/PCA analysis of the mean shapes. PC1 to PC3 summarize 88.2% of the total shape variation. The general disposition of taxa follows the previous comparisons (PC1 = differences between *Gorilla* and fossil taxa, PC2 = *Pongo* separated from *Homo*, PC3 separates humans from fossil taxa, see (figures 5.11 and 5.12). Both fossil taxa are closer to each other than is either to modern humans.

Mean *Homo ergaster* lumbar shape compared with modern hominoid means

The mean *Homo ergaster* lumbar vertebral shape was compared to modern lumbar mean shapes calculated from samples of juvenile and infant specimens of each taxon. Figure 5.14 shows a three-dimensional scatter plot of PC1 versus PC2 versus PC3 of the GPA/PCA analysis of these mean shapes. The three PCs summarize 95.3% of the total shape variation. PC1 discriminates between African apes, *and Homo ergaster*, *Homo sapiens*; PC2 separates all taxa from *Pongo,* and PC3 summarizes differences in mean shape between humans, *Homo ergaster* and *Pongo*.

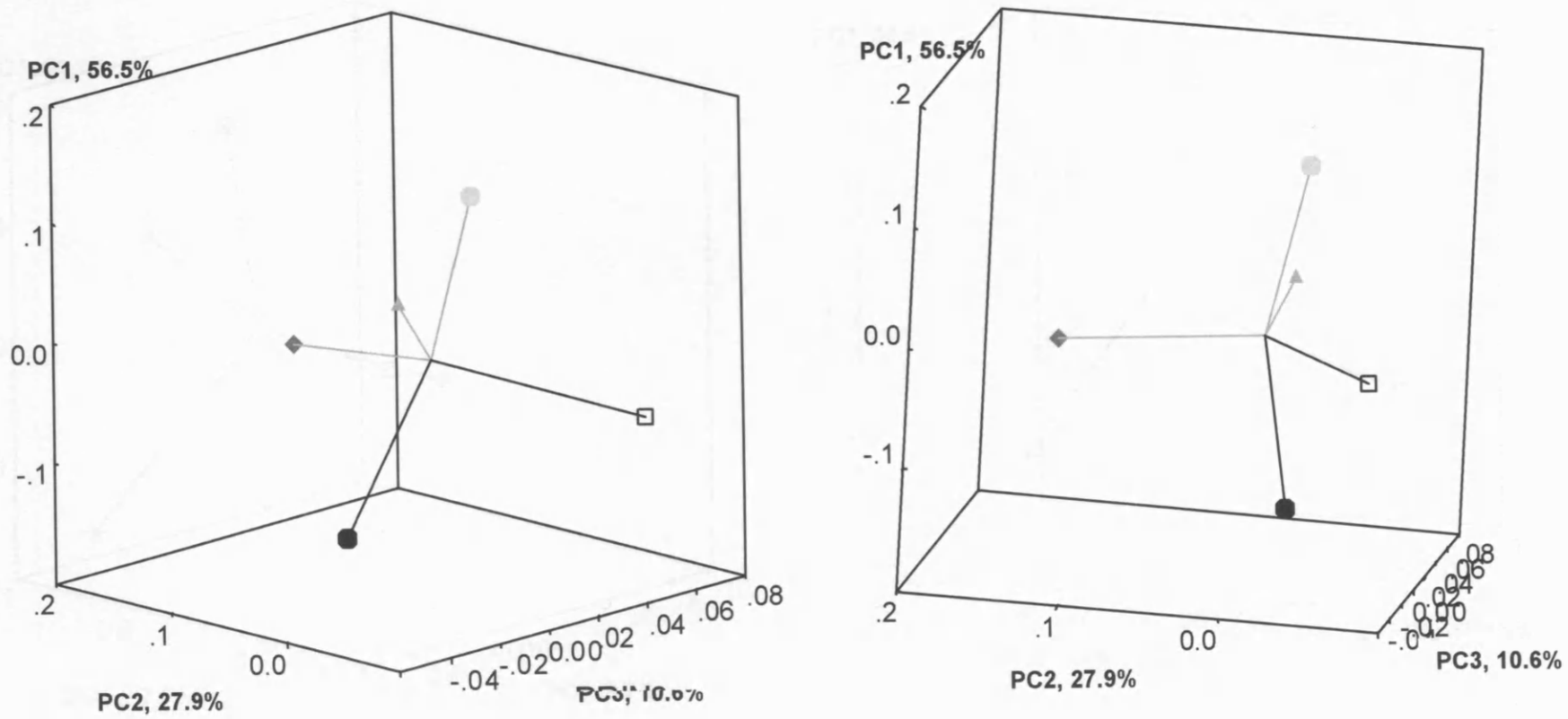


Figure 5.11 Scatter plot of PC 1 vs. PC2 vs. PC3 (56.5%, 27.9%, and 10.6%), mean shapes of modern taxa and mean *A. africanus* shape. ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*

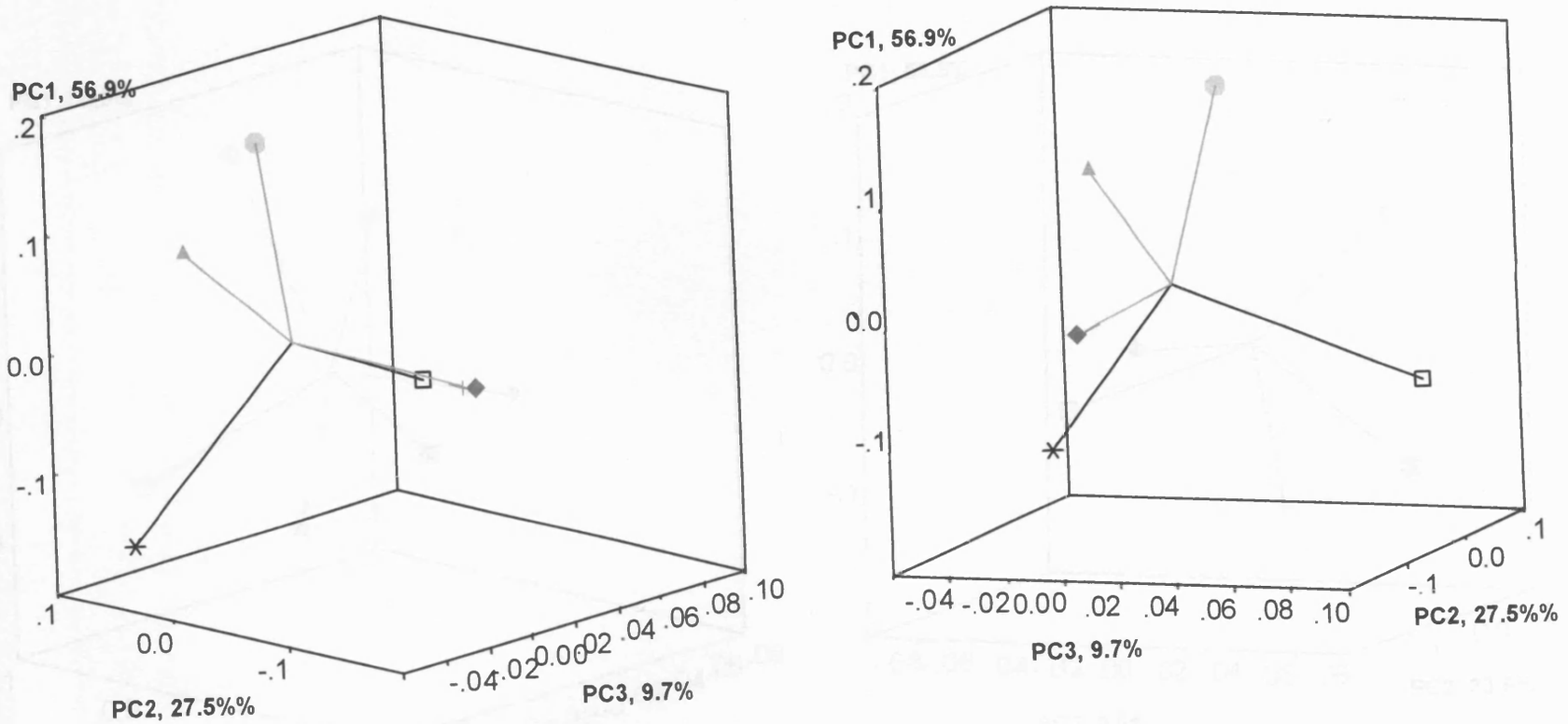


Figure 5.12 Scatter plot of PC 1 vs. PC2 vs. PC3 (56.9%, 27.5%, and 9.7%), mean shapes of modern taxa and *A. afarensis* AL288-1 at comparison level 2 (L2 great apes, L3 in humans and fossil hominins). ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, * = *A. afarensis*

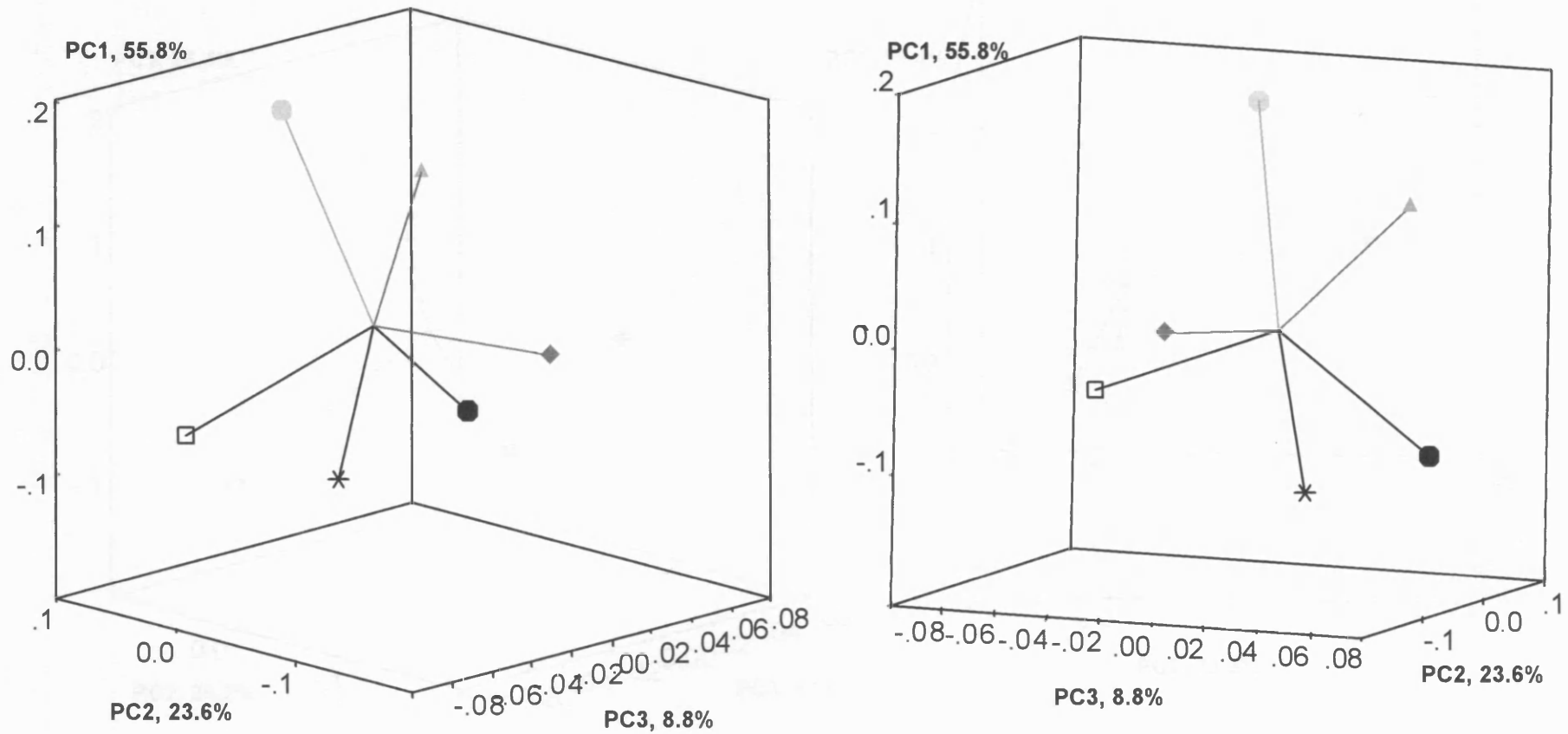


Figure 5.13 Scatter plot of PC 1 vs. PC2 vs. PC3 (55.8%, 23.6%, and 8.8%), mean shapes of modern taxa, mean *A. africanus* shape, and *A. afarensis* AL288-1 at comparison level 2 (L2 great apes, L3 in humans and fossil hominins). ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*, * = *A. afarensis*

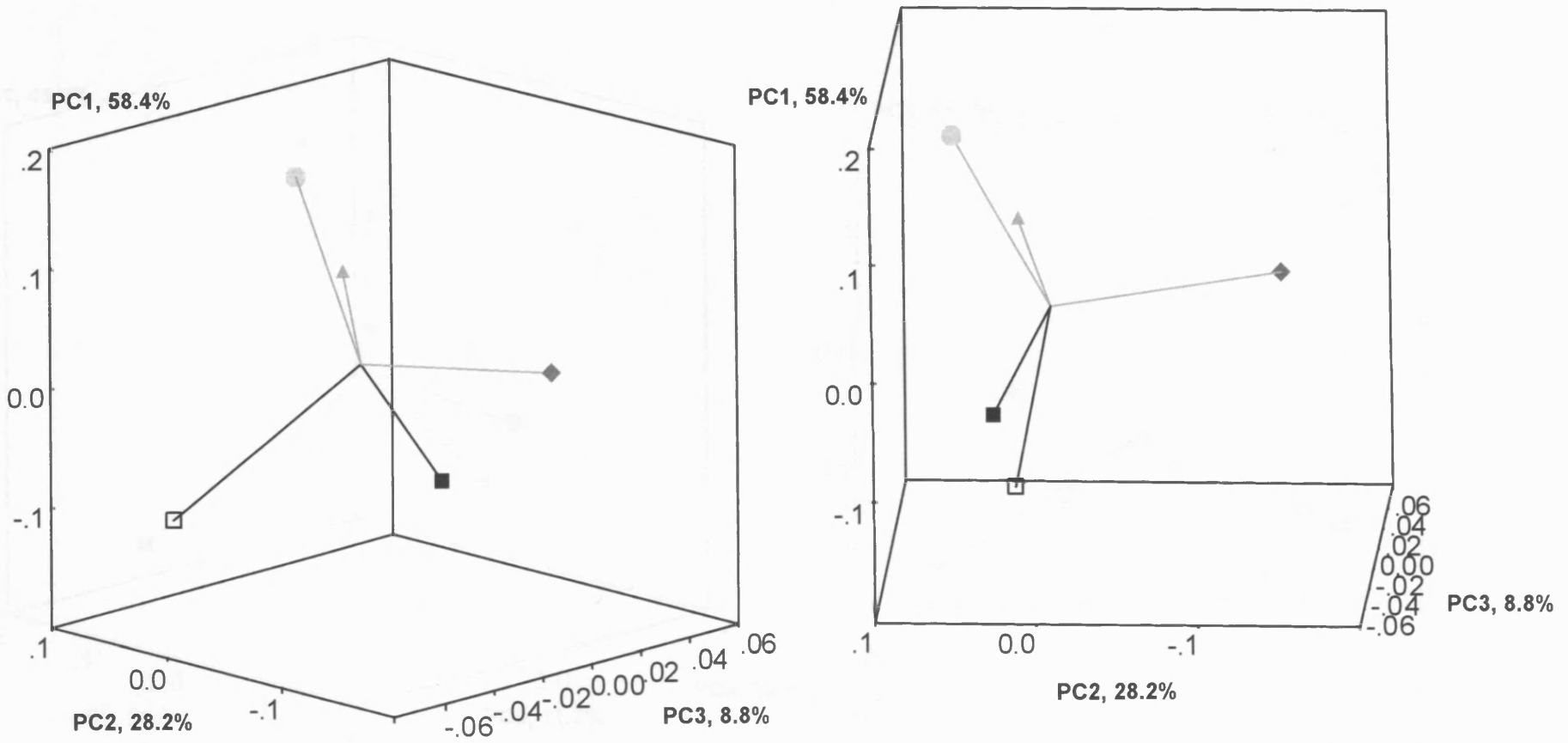


Figure 5.14 Scatter plot of PC 1 vs. PC2 vs. PC3 (58.4%, 28.2%, and 8.8%), mean shapes of modern taxa and *Homo ergaster,* specimen KNM-WT 15000. Sample consists of immature means for all taxa. ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ■ = *Homo ergaster*

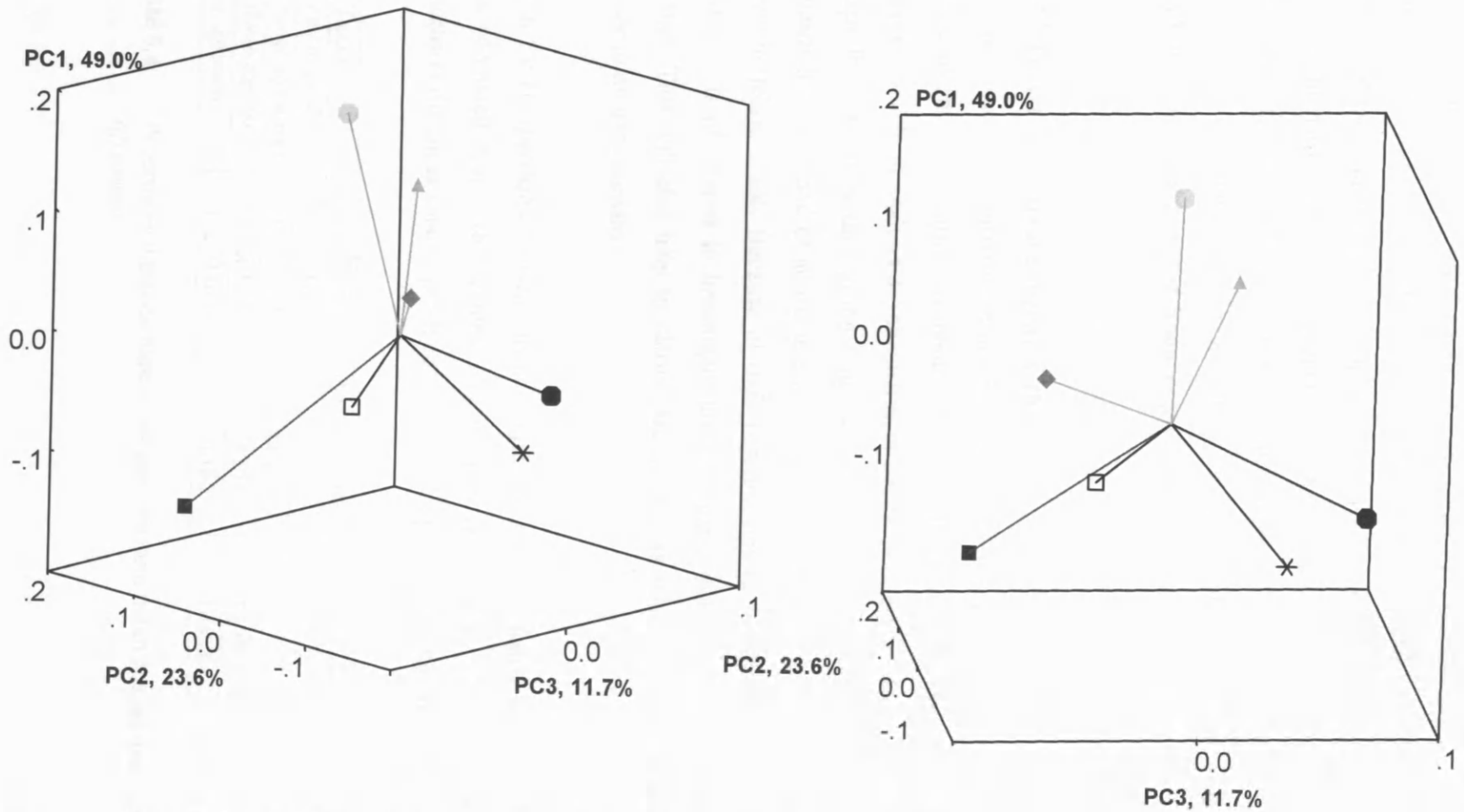


Figure 5.15 Scatter plot of PC 1 vs. PC2 vs. PC3 (49.0%, 23.6%, and 11.7%), at comparison level 2 for all mean shapes all taxa. ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*, * = *A. afarensis*, ■ = *Homo ergaster*

Comparison of all fossil mean shapes with modern hominoid means

In a final comparison, all fossil taxa, including the single *A. afarensis* and the juvenile *Homo ergaster* specimen were compared with the mean shapes of the modern taxa at comparison level 2. Figure 5.15 shows two views of a scatter plot of PC1 versus PC2 versus PC3 from the GPA/PCA analysis of these mean shapes. PCs 1 to 3 summarize 87.3% of the total shape variation. With all taxa entered, *Homo ergaster* is closest to modern humans – despite its juvenile age. The australopithecine taxa are separate from both humans and *Pongo* and closest to each other. PC1 separates African from Asian apes, humans, *Homo ergaster*, *A. africanus* and *A. afarensis*. PCs 2 and 3 seem to separate modern humans and *Homo ergaster* from the australopithecines.

5.4.8 Procrustes distances between the taxa

The previously presented three-dimensional scatter plots resulting from the GPA/PCA of means shapes of various combinations of fossil and modern taxa well illustrate what was less visible in analysis 3: the australopithecine taxa apparently are quite different in shape from all other taxa in the study. Of all the modern taxa, they resemble modern humans the most, and of all the great ape taxa, *Pongo* seems to resemble them most in mean vertebral shape. Because of their relationships to the *Pongo* and *Homo sapiens* means, it is of interest to investigate the Procrustes distances between species means further. This will also help to clarify issues such as which australopithecine taxon is closer to modern humans.

As in the comparison of species mean shape, the mean vertebral shape of *A. africanus* was compared first with the means of modern taxa. Table 5.4 shows the matrix of Procrustes distances used to produce the UPGMA phenogram in figure 5.16A.

Taxon	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*	*Homo sapiens*
Pan troglodytes	0.112569			
Pongo pygmaeus	0.218477	0.184335		
Homo sapiens	0.226121	0.174251	0.189570	
A. africanus	0.260305	0.193382	0.198788	0.132447

Table 5.4 Procrustes distance matrix, all modern taxa mean shapes and mean *A. africanus*

UPGMA phenograms were produced (see figure 5.16B) for the Procrustes distances between all modern taxa and *A. afarensis*, using the Procrustes distance matrix presented in table 5.5. Since *A. afarensis* is represented by a single third lumbar vertebra only, the comparison of Procrustes distances was conducted at comparison level 2 (L3 *Homo sapiens* and *A. afarensis*, L2 all great apes).

Taxon	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*	*Homo sapiens*
Pan troglodytes	0.131869			
Pongo pygmaeus	0.254513	0.214375		
Homo sapiens	0.252460	0.206064	0.220294	
A. afarensis	0.312278	0.251664	0.252041	0.154923

Table 5.5 Procrustes distance matrix, all modern taxa and *A. afarensis* at comparison level 2 (L3 and L2)

In a next step, the UPGMA phenogram was constructed for all modern taxa and both australopithecine taxa. Again, this comparison was conducted solely at comparison level 2. Table 5.6A presents the Procrustes distance matrix utilized for this comparison and the UPGMA phenogram is shown in figure 5.16C.

The Procrustes distance matrix shown in table 5.7 was used to produce a UPGMA phenogram for all modern taxa and *Homo ergaster*. Because the latter is a juvenile specimen, the mean shapes of modern taxa were calculated from samples consisting of infant and juvenile specimens. Infant and juvenile means compared to *Homo ergaster* gave similar results thus the full immature samples were used. The second lumbar vertebra of the *Homo ergaster* specimen is missing. Therefore, means for modern taxa were calculated excluding the second lumbar vertebra. The UPGMA phenogram for modern taxa and *Homo ergaster* is shown in figure 5.16D.

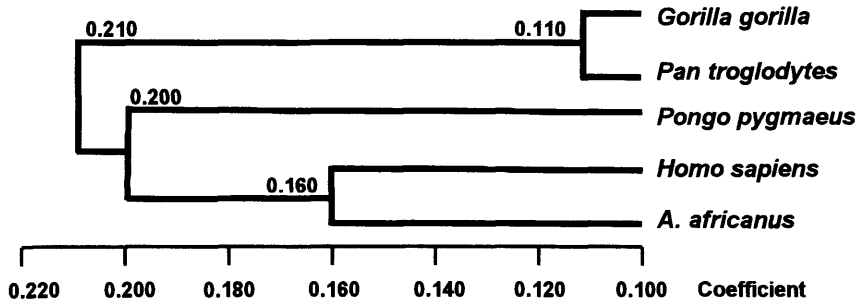
Table 5.6A

Taxon	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*	*Homo sapiens*	*A. africanus*
Pan troglodytes	0.131872				
Pongo pygmaeus	0.254562	0.214425			
Homo sapiens	0.252457	0.206061	0.220283		
A. africanus	0.284745	0.215343	0.222388	0.144225	
A. afarensis	0.312280	0.251649	0.252024	0.154908	0.143269

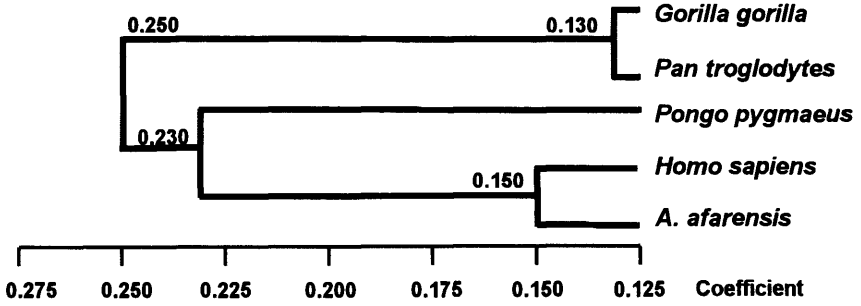
Table 5.6B

Taxon	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*	*Homo sapiens*	*Homo ergaster*
Pan troglodytes	0.119587				
Pongo pygmaeus	0.235698	0.179454			
Homo sapiens	0.252317	0.189164	0.206465		
Homo ergaster	0.285433	0.223849	0.245281	0.135520	
A. africanus	0.330827	0.253829	0.236572	0.182891	0.157960

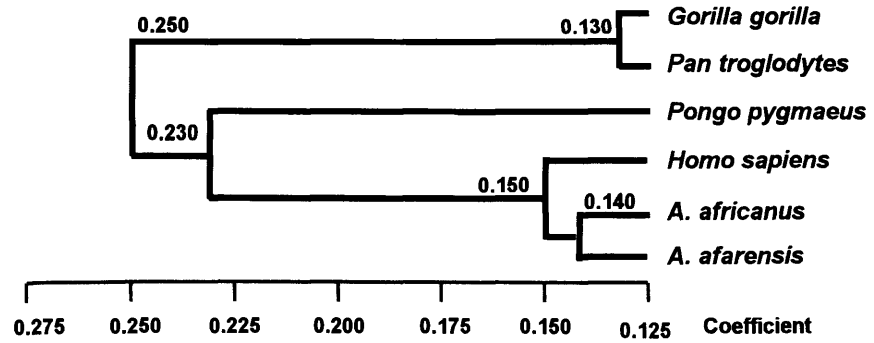
Table 5.6 Procrustes distance matrices calculated for comparisons of modern and fossil taxa. **(5A)** all modern taxa, and *A. africanus*, and *A. afarensis* at comparison level 2 (L3 and L2), **(5B)** all modern and all fossil taxa, at comparison level 2 (L3 *Homo sapiens* and fossils, L2 all great apes), all taxa except *Homo ergaster:* adult means



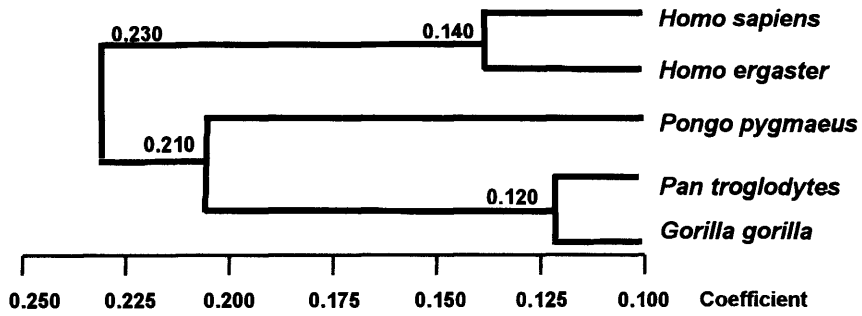
A: All modern taxa and *A. africanus* means MCC = 0.79803



B: All modern taxa and *A. afarensis*, Level 2 MCC: = 0.83481



C: All modern taxa and australopithecines, Level 2 MCC = 0.86603



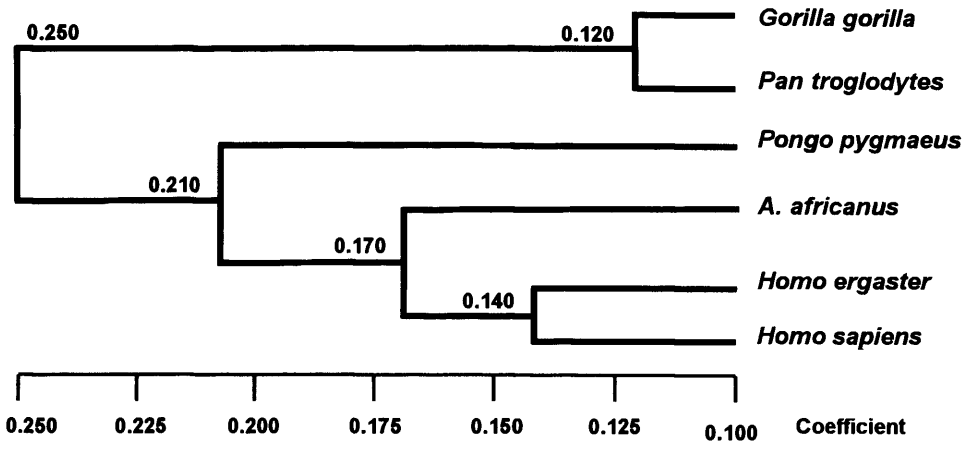
D: All modern taxa and *H. ergaster* means MCC: = 0.83228

Figure 5.16 UPGMA phenograms of Procrustes distances between combinations of modern and fossil taxa means at comparison level 2. Where Homo ergaster is included: modern taxa species means calculated from full immature samples and L2 excluded. Modern taxa and *A. africanus* **(A)**, modern taxa and *A. afarensis* **(B)**, modern taxa and both australopithecine taxa **(C)**, modern taxa and *Homo ergaster* **(D)**. MCC = Matrix correlation coefficient

Taxon	*Gorilla gorilla*	*Pan troglodytes*	*Pongo pygmaeus*	*Homo sapiens*
Pan troglodytes	0.119587			
Pongo pygmaeus	0.235694	0.179450		
Homo sapiens	0.252304	0.189159	0.206465	
Homo ergaster	0.285430	0.223852	0.245280	0.135526

Table 5.7 Procrustes distance matrix, all modern taxa and *Homo ergaster*, modern mean shapes calculated from infant and juvenile samples, L2 excluded in modern taxa because it is missing in *Homo ergaster*

Finally, the UPGMA phenogram was constructed for all modern taxa, *A. africanus* and *Homo ergaster*. Since both australopithecine taxa are quite similar to each other, only the *A. africanus* species mean was included in this analysis. This allowed the comparison of mean shapes. In the case of modern taxa, the mean shapes were calculated from full immature samples. The mean shape of L2 was excluded when calculating the species means. Only the mean shape of *A. africanus* was calculated from adult specimens. Table 5.6B presents the Procrustes distance matrix utilized for this comparison and the resulting UPGMA phenogram is shown in figure 5.17.



MCC = 0.80063

Figure 5.17 UPGMA phenogram of Procrustes distances between modern taxa, *A. africanus*, and *Homo ergaster* means. Modern taxa: species means calculated from full immature samples and L2 excluded. MCC = Matrix correlation coefficient

Results from this series of comparisons based on Procrustes distances show that the African apes are closest in mean shape to each other. *Pongo* is different from both,

African apes and a cluster formed by modern humans and all fossil taxa. Both australopithecine taxa are relatively similarly distant from modern humans and closer in shape to each other than to modern humans. Interestingly, humans and fossil mean shapes are more distant from each other than are those of the African ape taxa from each other. This is the case between humans and australopithecine taxa as well as between the two *Homo* taxa. However, the comparison of all taxa shows humans to be closest in shape to *Homo ergaster* and somewhat less close to australopithecine taxa. Matrix correlation coefficients (cophenetic correlations) were high for all comparisons of modern and fossil taxa (see figures 5.16 and 5.17) indicating that the phenograms reasonably well represent the distance matrices.

5.4.9 Analysis 5 description of differences in vertebral shape between fossil taxa, and selected modern hominoid taxa

The previous analyses show that there are differences in vertebral shape between modern and fossil taxa and that these are largest between the African apes and the fossil taxa. Between modern humans and the fossils, smaller differences in shape are observed. The australopithecines are more or less equidistant from *Pan* and *Pongo* and closer to *Homo* in the preceding distance matrices (see tables 5.4 and 5.6). In the present analysis, the nature of these lumbar vertebral shape differences between these four taxa will be explored. Additionally, differences in lumbar vertebral shape between the two *Homo* species will be described. This is because the available *Homo ergaster* specimen KNM-WT 15000 shows some pathological changes that should be assessed.

To visualize differences in shape between taxa, back projection and transformation grids (calculated by thin plate splines) were used after GPA/PCA on species mean data. Consistently, these grids were computed with the mean hominoid vertebral shape as the reference shape (located at co-ordinates 0/0/0) and the species means (*Homo ergaster*, *A. africanus*, *A. afarensis*, and *modern taxa*) as the target shape. These methods are the same as previously used in Chapters III and IV to visualize differences in vertebral shape intra-and inter-specifically.

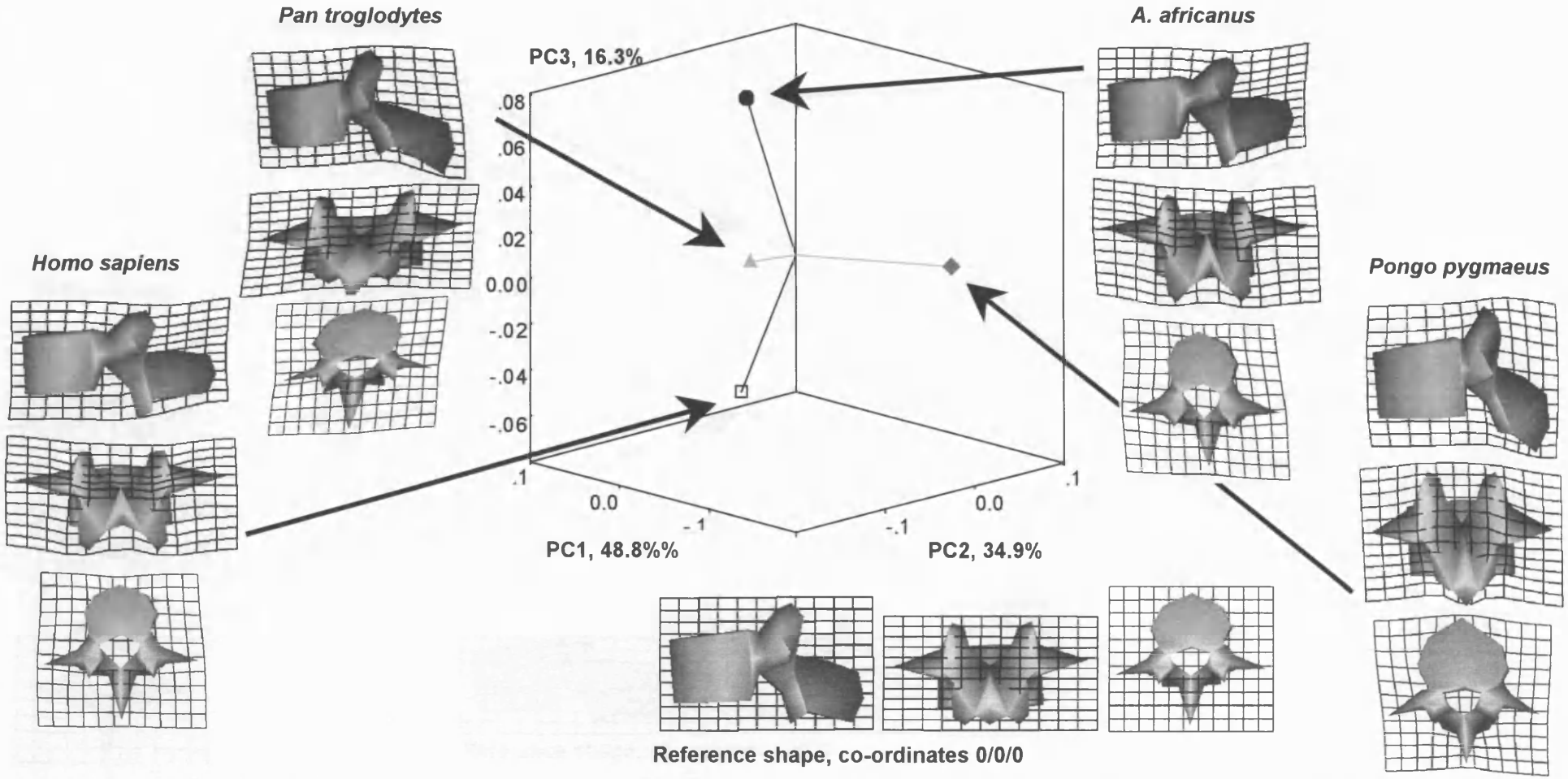


Figure 5.18 Scatter plot of PC1 vs. PC2 vs. PC3: inter-specific differences in shape between modern taxa and *A. Africanus*. Reference shape calculated from species means and located at coordinates (0/0/0), target shapes = species means of *Homo sapiens*, *Pongo pygmaeus, Pan troglodytes* and *A. africanus*. Left lateral, posterior, and superior views. Grid positions indicate greatest grid distortion. ◆ = *Pongo pygmaeus*, ▲ = *Pan troglodytes*, □ = *Homo sapiens*, ● = *A. africanus*

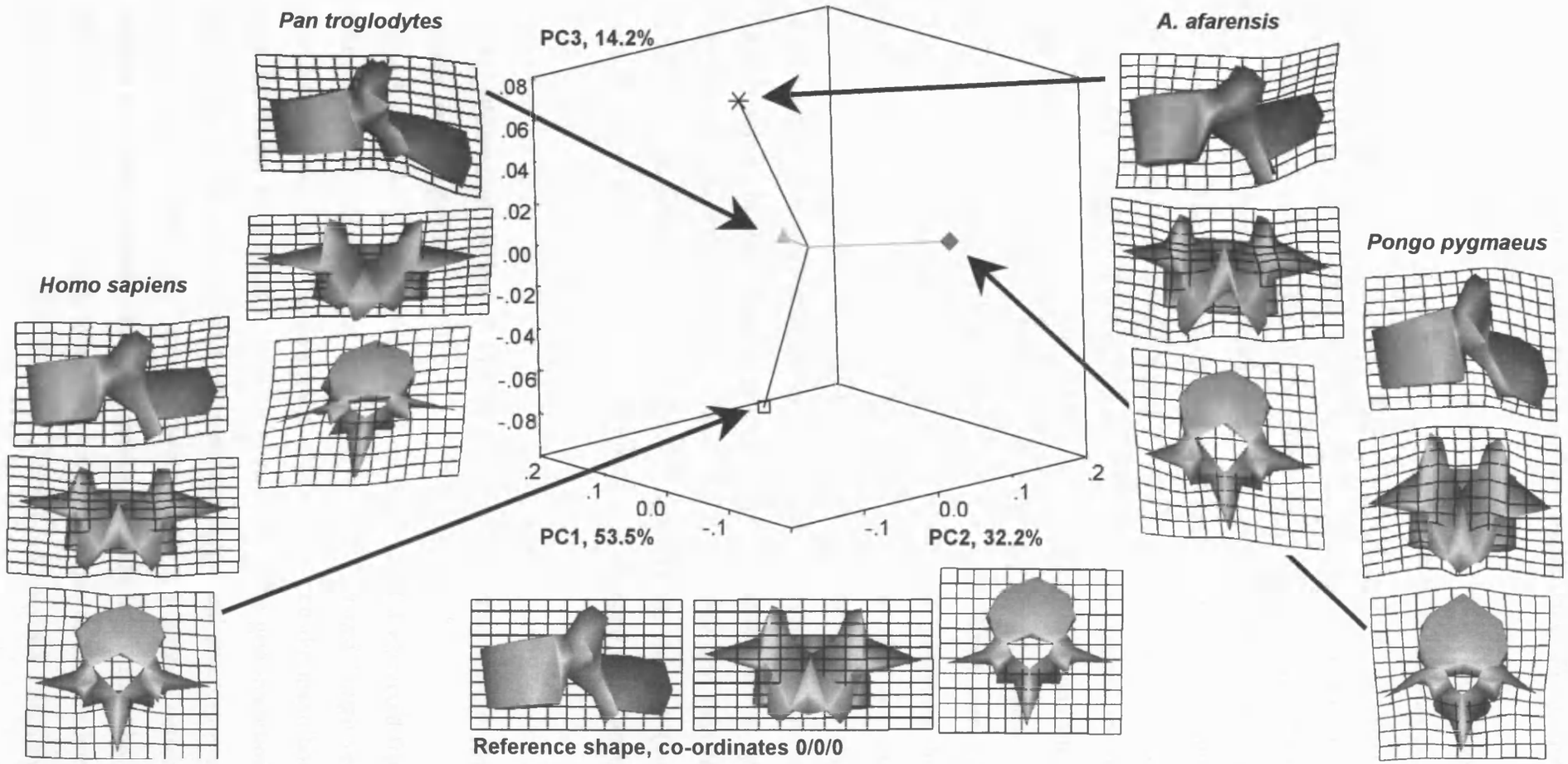


Figure 5.19 Scatter plot of PC1 vs. PC2 vs. PC3: inter-specific differences in shape between modern taxa and *A. Afarensis*. Reference shape calculated from species means and located at coordinates (0/0/0), target shapes = species means of L3 *Homo sapiens*, *A. afarensis* and L2 *Pan troglodytes* and *Pongo pygmaeus*. Left lateral, posterior, and superior views. Grid positions indicate greatest grid distortion. ◆ = *Pongo pygmaeus*, ▲ = *Pan troglodytes*, □ = *Homo sapiens*, ● = *A. africanus*

5.4.10 Differences in shape between *Pan troglodytes, Pongo pygmaeus, Homo sapiens,* and *A. africanus*

Figure 5.18 shows a scatter plot of PC1 vs. PC2 vs. PC 3 (100% tsv), extracted from GPA/PCA on species mean shapes (calculated from mean shapes at each lumbar vertebral level) of *Pan, Pongo, Homo sapiens*, and *A. africanus* together with transformation grids between each of these taxa and the mean hominoid shape (located at coordinates 0/0/0). The grid distortions shown in figure 5.18 indicate that of the four taxa, *A. africanus* has the relatively narrowest and antero-posteriorly relatively shortest vertebral bodies. The cranio-caudal lengths of the vertebral bodies seem to be relatively similar between the four taxa. However, *Pongo* and *Pan* to a lesser degree show anterior wedging of their vertebral bodies. Compared to the apes, humans and *A. africanus* have relatively longer and narrower pedicles. Compared to modern humans, the pedicles are relatively narrow but not different in relative length. Both, humans and *A. africanus* have relatively wider vertebral arches than the apes. When compared to the mean hominoid (co-ordinates 0/0/0), the superior articular processes are more widely separated in humans than in apes and in *A. africanus* they are intermediate. Both humans and *A. africanus* have relatively longer inferior articular processes than the mean hominoid whereas those of *Pan* and *Pongo* are relatively shorter. Humans have relatively longer inferior articular processes than *A. africanus*. *A. africanus* has the relatively longest costal processes, followed by *Pongo, Pan* and then *Homo sapiens*. In addition, *A. africanus* has the relatively longest (a-p), thinnest (c-c) and cranially orientated spinous process, followed *Homo sapiens, Pan* and then *Pongo*.

5.4.11 Differences in shape between *Pan troglodytes, Pongo pygmaeus, Homo sapiens,* and *A. afarensis*

Figure 5.19 shows a scatter plot of PC1 vs. PC2 vs. PC3 extracted from GPA/PCA of mean L3 *Homo sapiens* and, *A. afarensis*, and L2 *Pan* and *Pongo* vertebrae together with transformation grids between each of these taxa and the mean hominoid vertebral shape calculated from mean L2 and L3 respectively. The grid distortions in figure 5.19 indicate that *A. afarensis* has the relatively narrowest and antero-posteriorly shortened vertebral body of the three taxa. In addition, the L3 lumbar vertebral body of *A. afarensis* is funnel-shaped, with the superior endplate larger than the inferior. The *A. afarensis* pedicles are similar in relative length to those of modern humans (both have relatively longer pedicles than *Pan* and *Pongo*) but they are relatively narrower. The

vertebral canals of both humans and *A. afarensis* are relatively larger than those of the apes. In relation to this, humans and *A. afarensis* seem to have relatively broader vertebral arches than *Pongo* and, to a lesser extent, *Pan*. Both humans and *A. afarensis* have slightly relatively shorter superior articular processes than the mean hominoid (co-ordinates 0/0/0), whereas those of *Pongo* and *Pan* surpass those of the mean hominoid considerably in relative length. No difference is observed in the orientation of the superior articular facets between the taxa but those of humans and *A. afarensis* are relatively more widely separated. The relative length of the inferior articular processes of *Homo sapiens* and *A. afarensis* is greater than in the mean hominoid and apes. There seems to be no difference in the degree of posterior angulation of the inferior articular processes between the three taxa. However, *A. afarensis* appears to have the relatively widest opening of the *Incisura vertebralis major*. This is due to the pronounced funnel-shape of its vertebral body. Although there is some asymmetry observed in the length of the inferior articular processes of *A. afarensis* (probably due to taphonomic processes), the tips of these processes are relatively farther apart than those of modern humans. The costal processes of *A. afarensis* cannot be compared securely because they were both missing and had to be reconstructed (*A. africanus* has been used as a model). Of all the taxa, *A. afarensis* has the relatively longest spinous process. However, there seems to be no difference in relative spinous process height between humans and *A. afarensis*. Compared to the modern taxa, the spinous process of *A. afarensis* is most cranially orientated.

5.4.12 Differences in vertebral shape between *Homo ergaster* and the modern taxa – assessing shape differences in relation to a pathological condition in the *Homo ergaster* specimen

Previous analyses show that of all the fossil taxa, *Homo ergaster* resembles *Homo sapiens* the most. However, the African ape taxa, although less closely related to each other (according to genetic analysis) resemble each other more than the two *Homo* taxa. This result comes as a bit of a surprise and therefore further investigation of the differences in shape between *Homo sapiens* and *Homo ergaster* have been undertaken. This is because the juvenile status of the *Homo ergaster* specimen might account for some of the differences observed between the two *Homo* taxa. Furthermore, the state of preservation of the *Homo ergaster* fossil (e.g. endplates of vertebral bodies are missing in the *Homo ergaster* specimen) might account for the differences in relative vertebral

body length. Finally yet importantly, the lumbar vertebrae of the *Homo ergaster* specimen show morphology that cannot be explained by taphonomic processes but highly likely are attributable to pathology. Therefore, the species mean shape has been calculated from the *Homo sapiens* juvenile sample (excluding L2) and compared to the mean shape calculated from the four available *Homo ergaster* lumbar vertebrae. The differences between the two mean shapes are presented in figure 5.20.

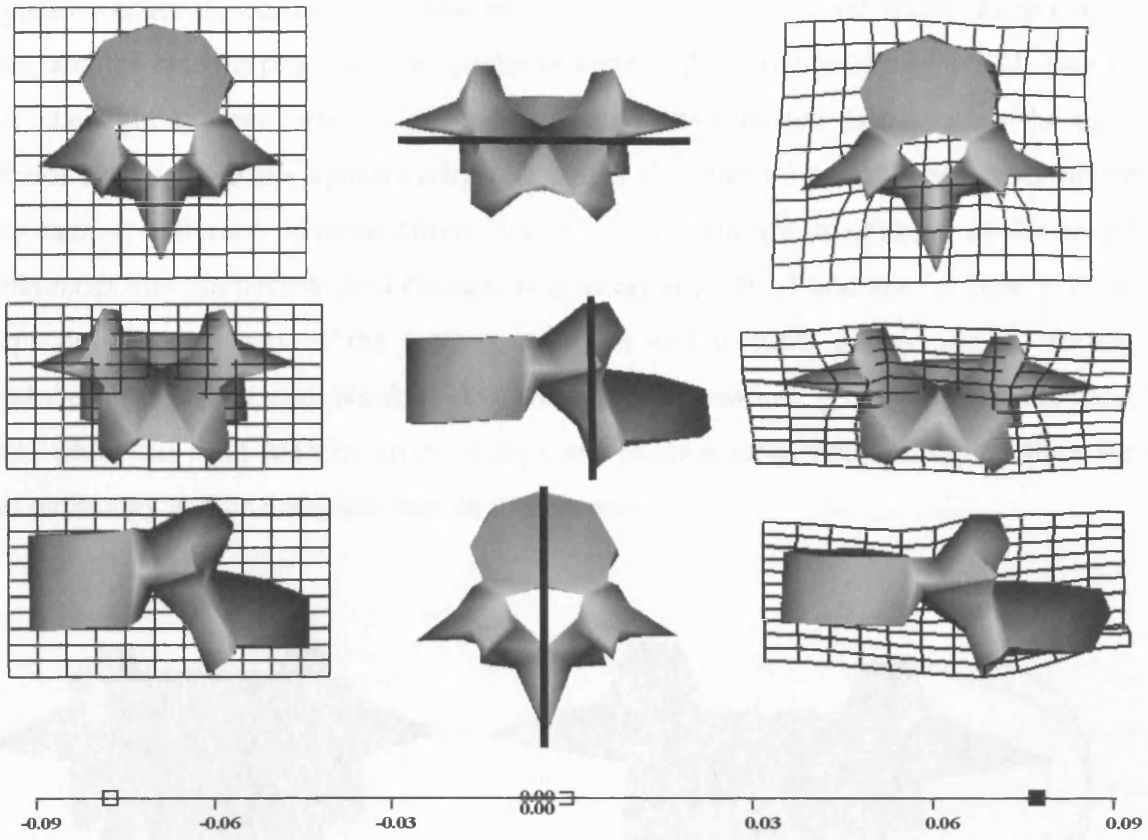


Figure 5.20 Differences in shape between species means of juvenile *Homo sapiens* and mean shape of *Homo ergaster*. Superior, posterior, and left lateral views (top to bottom). Grid positions indicate greatest grid distortion, reference shape: □ = *Homo sapiens*, target shape: ■ = *Homo ergaster*

Differences in shape between juvenile modern human and the *Homo ergaster* specimen *not* attributable to pathology consist of the observations that *Homo ergaster* seems to have relatively narrower, cranio-caudally compressed and antero-posteriorly longer vertebral bodies than modern *Homo sapiens*. The costal processes are relatively longer in *Homo ergaster* than in modern humans. The exception from this is the costal processes of the last lumbar. No difference in relative process length is observed at this particular comparison level. In both species, the decrease in costal process length is

accompanied by an increase in costal process robusticity at level L5. The spinous process is relatively longer in *Homo ergaster* than in *Homo sapiens*. Furthermore, the inferior articular processes of *Homo ergaster* are relatively shorter. The superior articular processes, on the other hand, are relatively longer in *Homo ergaster* than in *Homo sapiens*.

Differences in shape between the two *Homo* taxa (likely pathology in the *Homo ergaster* vertebrae) consist of an asymmetric twist of the vertebral body, the vertebral arch, and the spinous process in the posterior view of the vertebra of figure 5.21. Due to this, the right superior articular process is shorter than the left one whereas the right inferior articular process appears relatively longer than the left one. Comparisons of the two taxa at different vertebral levels (L1, L2...) reveals the magnitude of the shape differences due the pathological changes is greatest at level L1 and least at level L5. On inspection of the casts of the lumbar vertebrae and pictures of the original fossils, published by Latimer and Ward (1993) one notices a marked groove on the vertebral arch, where the right superior articular facet and process meet. Possible explanations for this pathology will be discussed later in this chapter.

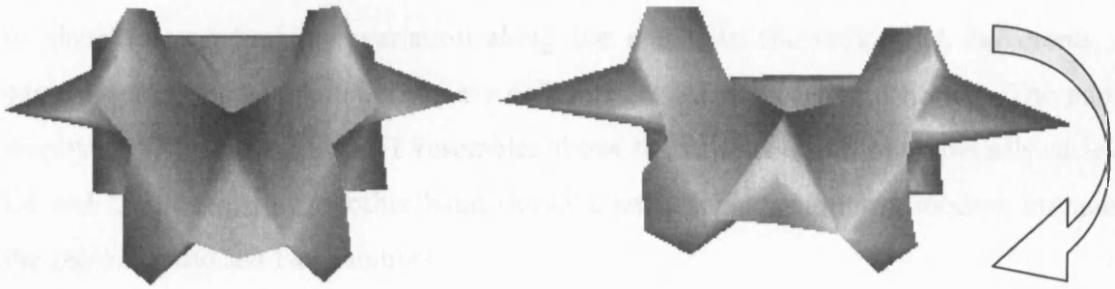


Figure 5.21 View of pathological shape of *Homo ergaster* KNM-WT lumbar vertebrae (mean shape) in comparison to the mean *Homo sapiens* juvenile shape. The arrow indicates direction of twist observed in vertebral body and arch. Posterior view

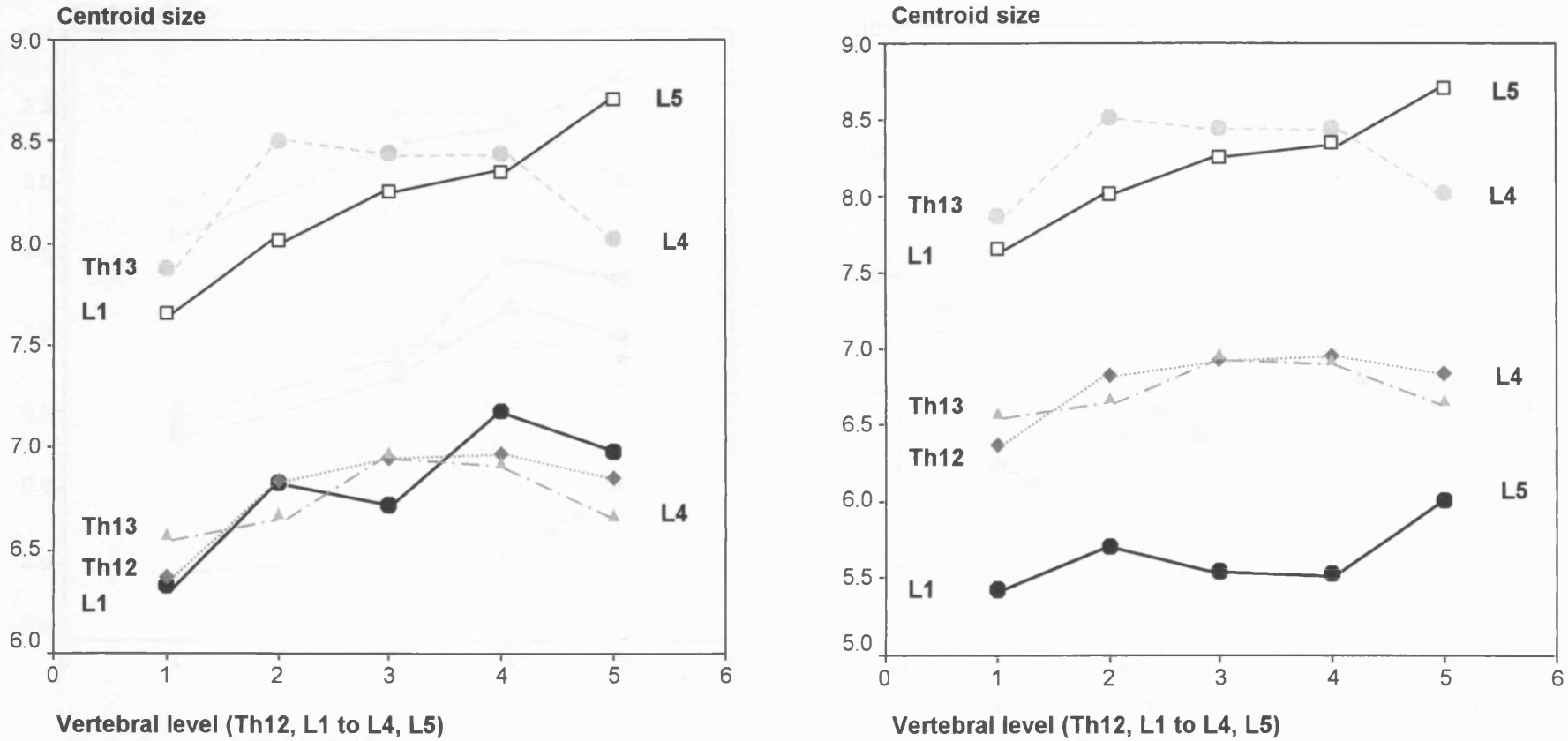
5.4.13 Analysis 6, comparison of patterns of inter-segmental size and shape variation along the lumbar spine between modern and fossil taxa

In contrast to previous analyses, analysis 6 investigates patterns of vertebral size and shape variation along the lumbar spine between modern and fossil taxa. The first

analysis explores patterns of vertebral size variation between modern taxa and *A. africanus*. The next, the patterns of vertebral size variation between all modern taxa, *A. africanus* and *Homo ergaster* are explored. Only four lumbars were used to examine metameric patterns of size variation where the *Homo ergaster* specimen was included. Although *Homo ergaster* is a juvenile specimen it has been compared here with adult mean shapes. This should not pose a problem since *patterns* of size and shape variation should be the same for juvenile as well as adult specimens at least this was the case in comparison of patterns in Chapter III, (pp. 267-268). *A. afarensis* was not included in any of these comparisons since it consists of only one lumbar vertebra.

5.4.14 Differences in patterns of vertebral size variation along the lumbar spine between *A. africanus* and modern taxa

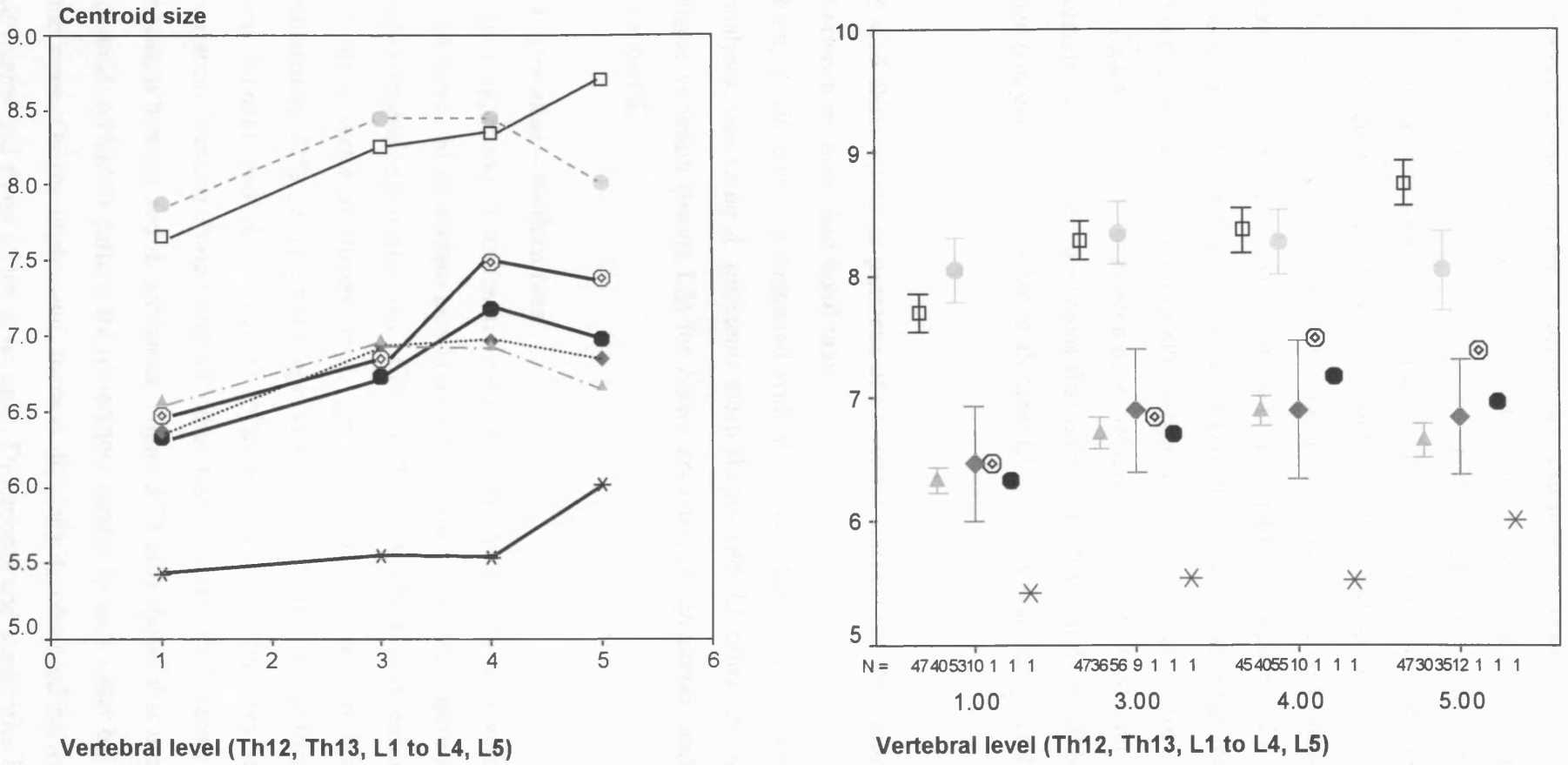
The two *A. africanus* specimens Sts14 and Stw431 were entered separately into this comparison. This was performed as specimen Sts14 (especially its last lumbar) was reconstructed by Robinson (1972) using *Homo sapiens as* a model. Figure 5.22 shows scatter plots of mean vertebral centroid sizes (y-axis) versus vertebral levels (x-axis). Figure 5.22A depicts the comparison of modern taxa with *A. africanus* Stw431 and 5.22B that of modern taxa with Sts14. Neighbouring vertebrae are connected with lines to visualize vertebral size variation along the spine. In the case of *A. africanus*, the patterns of vertebral size variation are different between the two specimens. The pattern displayed by specimen Stw431 resembles those of modern ape taxa, especially at levels L4 and L5. Sts14, on the other hand shows a pattern that resembles modern humans in the region of the last two lumbars.



A: centroid size variation pattern of Stw431

B: centroid size variation pattern of Sts14

Figure 5.22 Inter-specific differences in patterns of vertebral size variation along the lumbar spine between modern taxa and *A. africanus*. Scatter plots of centroid size vs. vertebral levels L1 to L5 in humans and *A. africanus* and Th12/Th13 to L4 in great apes. Left side **(A)** includes *A. africanus* specimen Stw431, right side **(B)** includes A. africanus specimen Sts14. Note the differences between patterns of the two *A. africanus* specimens. □ = *Homo sapiens*, ▲ = *Pan troglodytes*, ● = *Gorilla gorilla*, ◆ = *Pongo pygmaeus*, ● = *A. africanus*



A: Size pattern differences between modern and fossil taxa

B: 95% CI centroid size variation patterns modern taxa and fossils

Figure 5.23 Inter-specific differences in patterns of vertebral size variation between all modern taxa, *A. africanus* and *Homo ergaster*. Centroid size plotted against vertebral levels L1, Th12, and Th13 to L5 and L4 **(A)**. 95% confidence interval centroid size vs. vertebral levels (n = 584) **(B)**. □ = *Homo sapiens*, ▲ = *Pan troglodytes*, ● = *Gorilla gorilla*, ◆ = *Pongo pygmaeus*, ● = *A. africanus* specimen Stw431, * = *A africanus* specimen Sts14, ⊙ = *Homo ergaster*

5.4.15 Differences in patterns of vertebral size variation along the lumbar spine between *Homo ergaster*, *A. africanus*, and modern taxa

Next the metameric pattern of vertebral size variation of *Homo ergaster* was compared with those of modern taxa and *A. africanus*. Figure 5.23A shows the patterns of vertebral size variation, all lacking L2, for all modern taxa whereas figure 5.23B shows the 95% confidence interval for each vertebra and modern taxon. As noted above Stw431 resembles great apes the most; *A. africanus*, Sts14 shows a very human-like pattern of vertebral size variation. The pattern displayed by the *Homo ergaster* specimen KNM-WT 15000 shows a caudal increase in size but differs from the human mean in that L5 is not appreciably larger than L4. The pattern for *Homo ergaster* shown in figure 5.23A most resembles *A. africanus* Stw431. It should be noted that in the sample of 44 human specimens that possess both L4 and L5, all but 3 (7%) specimens had a larger L5 than L4 but in all cases L5 was only marginally smaller than L4.

5.4.16 Differences in patterns of vertebral shape variation along the lumbar spine between modern and fossil taxa

First, *A. africanus* is compared with all modern taxa. This is carried out through two analyses, one using *A. africanus* mean shapes and the other, the metameric patterns of shape variation (minus L2) for *Homo ergaster*, *A. africanus*, and all modern taxa are compared.

A. africanus – modern taxa

The comparison of metameric patterns of mean *A. africanus* vertebral shape variation with means of all modern taxa is shown in figure 5.24. The figure shows two views of a three-dimensional scatter plot of PCs 1, 2, and 3, which were extracted from GPA/PCA of mean vertebral shapes of *A. africanus* and the modern taxa. These three PCs summarize 72% of the total shape variation. PC1 separates African apes from *Pongo*, and humans and *A. africanus*. PC2 summarizes differences in patterns of shape variation between *Pongo* and all other taxa. Finally, PC3 seems to best discriminate between humans and *A. africanus*. Figure 5.24 also shows that modern humans and the mean *A. africanus* pattern are remarkably similar to each other but they are not entirely the same. On the other hand, there is dissimilarity observed between the pattern of *A. africanus* and those of the great apes. Differences and similarities in metameric patterns

of vertebral shape variations between humans and *A. africanus* will be described later in this chapter.

***Homo ergaster* – *A. africanus* and modern taxa**

In a this comparison, metameric patterns of vertebral shape variation (not including L2) were compared between the available *Homo ergaster* specimen, *A. africanus* and the modern taxa. Figure 5.25 shows two views a three-dimensional scatter plot of PCs 1, 2, and 3 (summarizing 67% tsv in all), extracted from GPA/PCA of mean shape data (modern humans and *A. africanus*). As before, PC1 best discriminates between humans plus the fossil taxa, *Pongo*, and the African apes. PC2 separates *Pongo* from all other taxa and PC3 best separates *A. africanus* from both *Homo sapiens* and *Homo ergaster*. The metameric pattern of vertebral shape variation is very similar between humans and *Homo ergaster* and between humans and *A. africanus*. As in previous comparisons of patterns of shape variation, none of the patterns displayed by fossil taxa resembles any of the great apes. Nevertheless, one can see (figure 5.25) that the pattern of *A. africanus* – although similar to modern humans – is still somewhat different.

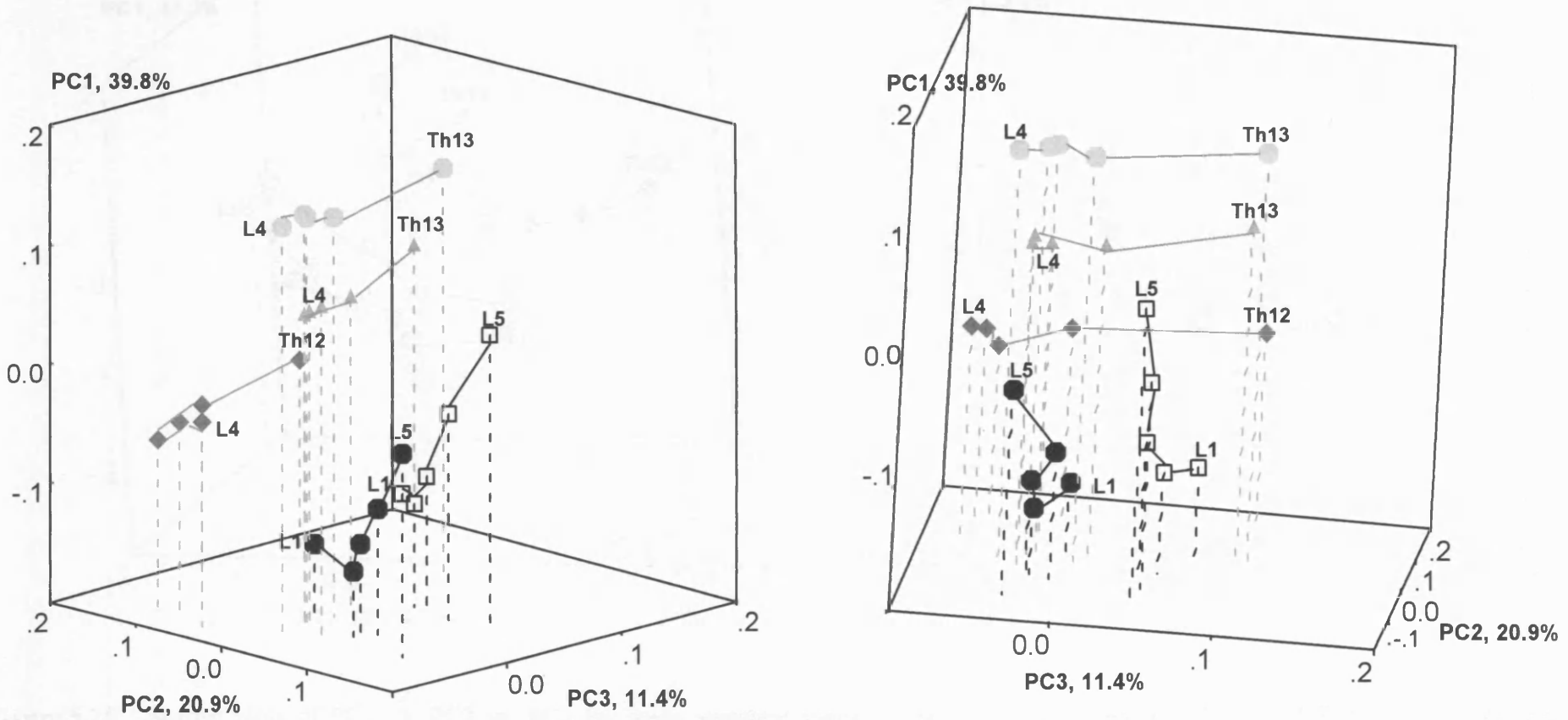


Figure 5.24 Scatter plots of PC1 vs. PC2 vs. PC3 for mean vertebral shapes at each vertebral level (L1, Th12 and Th13 to L5, L4), visualizing patterns of metameric shape variation of modern taxa and *A. africanus*. Consecutive vertebrae of each taxon are connected. First and last vertebrae of each series are marked. ● = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*

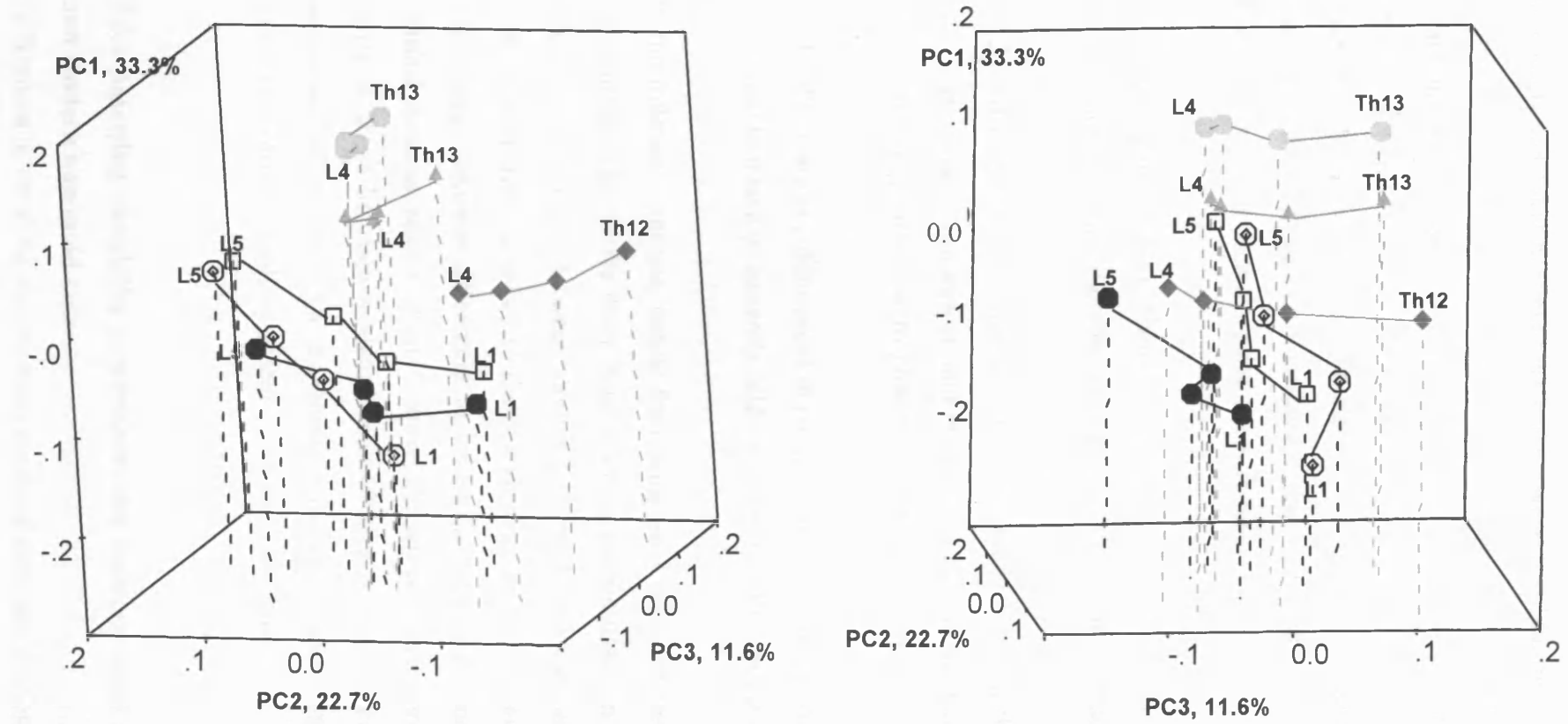


Figure 5.25 Scatter plots of PC1 vs. PC2 vs. PC3 for mean vertebral shapes at each vertebral level (L1, Th12 and Th13 to L5, L4), visualizing patterns of metameric shape variation of modern taxa, *A. africanus*, and *Homo ergaster*. Consecutive vertebrae of each taxon are connected. First and last vertebrae of each series are marked; L2 not present. ○ = *Gorilla gorilla*, ▲ = *Pan troglodytes*, ◆ = *Pongo pygmaeus*, □ = *Homo sapiens*, ● = *A. africanus*, ⊙ = *Homo ergaster*

5.5. Discussion

This study has examined differences in vertebral size and shape between modern hominoids and fossil hominin taxa and between fossil hominins. The aims of the studies as presented in the introduction of this chapter are to assess the variations between australopithecine fossils to see if they are consistent with the current view of two species, *A. africanus* and *A. afarensis*, and second to assess the similarities and differences between the fossil and modern taxa. Both of these analyses are then used to assess any likely differences in locomotion between fossil and modern taxa. The aims of study are presented once more and are as follows:

1. To assess the variability in vertebral size and shape in the lumbar vertebral column of *Australopithecus* relative to that found in modern taxa

2. To assess the differences in size and shape between the fossil hominin taxa *A. africanus*, *A. afarensis*, and *Homo ergaster* and the modern taxa *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*

3. To relate any differences in size and shape between fossil and between fossil and modern taxa to currently held views on their locomotor repertoires

In the following sections, results from analyses 1 to 6, addressing the above aims, are summarized. The results from these analyses are discussed in relation to differences in locomotor repertoires between modern hominoid taxa and between fossil and modern taxa as have been reviewed in the introduction of the present chapter. The focus on relationships between differences in locomotion and differences in vertebral shape is justified because results from Chapter IV indicate that inter-specific differences in vertebral shape between modern hominoid taxa principally provide information about locomotor differences. This discussion is organised according to the study aims and follows the order of analyses as laid out in the result section.

5.5.1 Assessing variability in vertebral size between fossil taxa and between fossil and modern hominoid taxa

Differences in vertebral size between the fossil taxa and the fossil and modern taxa were examined in analysis 1. The analysis addressed two different types of size differences:

first, inter-specific differences between modern and fossil taxa, and between fossil taxa and second, intra-specific differences in vertebral size within *A. africanus* in relation sexual size dimorphism observed in modern taxa.

The comparison of vertebral centroid size between all fossil taxa indicates that *Homo ergaster* differs from all the australopithecine specimens in vertebral size: *Homo ergaster* shows considerably larger lumbar vertebrae than *Australopithecus*. The australopithecine taxa do not differ considerably in vertebral size.

Results from the comparison of fossil and modern taxa indicate that vertebral size of *Homo ergaster* surpasses that of *Pan* and *Pongo* (both sexes) and lies within the 95% confidence limits of female *Gorilla*. Results from analysis 2 comparing *Homo ergaster* vertebral centroid size and shape with that of modern humans further underline the similarity in vertebral size between specimens of comparable age. It is likely then, that, had this particular specimen reached adulthood, its vertebral size would have been within the ranges of *Gorilla* and *Homo sapiens*. The centroid size of the australopithecines is in general similar to that of *Pongo* and *Pan* but smaller than that of *Gorilla* and *Homo sapiens*.

Since Sts14 might be a female *A. africanus* specimen, whereas specimens Stw8, 431, and 572 might be male, potential sexual dimorphism in vertebral size of *A. africanus* was compared with sexual dimorphism observed in the modern hominoid taxa. Results show that compared to the modern taxa, sexual dimorphism in mean vertebral centroid size of *A. africanus* would lie well within the range of sexual dimorphism expressed in modern taxa. *Gorilla* and *Pongo* vertebrae are more size dimorphic than those of *A. africanus* which in turn would be more dimorphic than those of *Homo sapiens* and *Pan*. Using the body weight estimations for *A. africanus* by McHenry (1992a, b), the ♂/♀ weight ratio calculated is equal to that of *Pan* (see table 5.1). Compared to *Pan*, *A. africanus* would show considerably more sexual dimorphism in vertebral size. In this, *A. africanus* resembles modern humans, where relatively large differences in vertebral size are paired with the smallest ♂/♀ weight ratio. In humans, this is interpreted as a consequence of habitual upright trunk posture, because in this posture even a relatively small sexual weight dimorphism can have a high impact on vertebral size (vertebral column as the sole weight support structure in the trunk, see chapter I for more details). However, it should be borne in mind that the modern taxa are represented by means

whereas the fossil comparison is between individuals. Mean differences do not reflect the range of differences between any two individuals of different sex so these findings do not necessarily reflect sexual dimorphism.

Differences in vertebral size between australopithecine taxa

The third lumbar vertebral centroid size of both australopithecine taxa in the study is similar. Since the present *A. afarensis* sample only contains this one vertebra (AL 288-1), it is difficult to assess the vertebral size variation of this particular taxon. However, other *A. afarensis* lumbar vertebrae (not available for the present study) are reported to be larger than that of AL 288-1 (Cook, 1983; Sanders, 1998). In the present study, vertebral size is not a feature sufficient to distinguish the two australopithecine taxa. The overall size of australopithecine lumbar vertebrae is not different from *Pongo* and *Pan* – with the exception of the small sized *A. africanus* specimen Sts14. The results of the present study agree with the findings of Sanders (1998), that australopithecine lumbar vertebrae are similar in size to those of *Pan* and *Pongo*.

Differences in vertebral size between fossil hominins and modern hominoid taxa

In vertebral size, *Homo ergaster* resembles older (aged 17 years) juvenile human specimens the most. The small differences in vertebral size between humans and *Homo ergaster* are not surprising. Both taxa share similar body proportions and potentially body weight (Bramble and Lieberman, 2004; Ruff and Walker, 1993; Wang et al., 2004). Compared to great apes, the *Homo ergaster* vertebrae are similar in vertebral size to *Gorilla* juvenile specimens (aged approximately 5 to 7 years) and subadult *Pongo* specimens (aged approximately 8 to 11 years).

All modern hominoid primates are characterized by having relatively larger vertebrae (in particular lumbars) than non-hominoid primates (Rose, 1975; Schultz, 1953; Schultz, 1961; Schultz and Straus, 1945). Australopithecine vertebrae fall well within the 95% confidence limits of vertebral size of several modern hominoid taxa – a result, which should be expected, based on their estimated body size and body proportions, which are similar to hominoids. The comparative studies of vertebral centroid size presented in Chapter IV, as well as works by other authors (Cook, 1983; Robinson, 1972; Rose, 1975; Sanders, 1994; Schultz, 1931) conclude that humans have larger lumbar vertebrae than would be expected for a hominoid of their body size. The body weight of australopithecines is not known. Estimations of their body weight differ

considerably depending on the postcranial part of the skeleton the weight estimation is based on Jungers (1991), McHenry (1991b), and McHenry and Berger (1998). In this study no conclusions are drawn about whether australopithecines had lumbar vertebrae which are of an expected for their body weight. Nevertheless, previous studies seem to agree that australopithecines have relatively small lumbar vertebrae for their estimated body weight (Jungers, 1991; Sanders, 1998; Shapiro, 1993a). *Homo sapiens* and *Homo ergaster* are therefore the only hominoid taxa whose vertebral size is larger than would be estimated for their body weights. As discussed in Chapter IV This relates to upright trunk posture and bipedal gait. If australopithecines exhibited habitual upright trunk posture and locomotion as in modern humans one might anticipate that they would have larger than expected lumbar vertebrae. Alternatively, it could be argued that only *Homo* – highly specialized in long distance and bipedal running combined with relatively large body weight – is in need of disproportionally enlarged vertebrae. This is because running and presumably transporting loads in combination with relatively large body weights create larger peak loads in the lumbar vertebrae. Australopithecines in contrast have body proportions (in particular upper limbs and thorax) which are rather different from modern humans and are presumably not adapted for long distance running and modern human-like bipedal walking. Their vertebrae might therefore not be subjected to the same amount of peak loads as in modern humans. Australopithecines are relatively smaller than modern humans. Therefore, they might not need the large lumbars as seen in modern humans to support their body weight. This would be consistent with the current view that their vertebrae are not exceptionally large.

Sexual dimorphism in *A. africanus*

In contrast to the skull (great apes) and the pelvis (modern humans), the lumbar spine of modern hominoids is of less diagnostic value in relation to sexual dimorphism. Nevertheless, differences in vertebral size are observed within the sexually dimorphic modern hominoid taxa. The differences in size are related to the degree of sexual body weight dimorphism: largest differences in vertebral size are observed in *Gorilla* and *Pongo*, followed by *Homo* and *Pan*. Differences in vertebral size observed in *A. africanus* in the present study – if they represent sexual dimorphism – are in accordance with the outcome of the study of sexual dimorphism of the *A. afarensis* postcranium by Lockwood et al. (1996b) and McHenry (1991b; 1991c). The intra-specific differences in vertebral size observed thus indicates the possibility of a degree of sexual dimorphism

intermediate between that observed in strongly sexually dimorphic taxa (*Gorilla, Pongo*) and the moderately dimorphic modern humans in *A. africanus*.

5.5.2 Assessing variability in vertebral size between fossil taxa and between fossil and modern hominoid taxa

Differences in vertebral shape between modern and fossil taxa were explored in analyses 2, 3, and 4. Additionally, these analyses provided some insight into differences in vertebral shape between the fossil taxa. Analysis 2 explored the differences in single lumbar vertebral shape between modern and fossil taxa at various comparison levels. *Homo ergaster* was separately compared to samples containing both adult and immature specimens of modern hominoid taxa. Analysis 3 compared various combinations of species mean shapes (modern and fossil taxa) with each other and analysis 4 further explored Procrustes distances between species means.

Differences in vertebral shape between the australopithecine taxa

Differences in shape between the australopithecine taxa are small. The magnitude of shape differences is close to that observed between the two African ape means. This could indicate that, based on lumbar vertebral shape, *A. africanus* and *A. afarensis* are indeed two different species. Similar results are reported from other postcranial regions. For example, Häusler (2002; 2001) finds overall a large degree of similarity in pelvic morphology between *A. afarensis* and *A. africanus* despite other important differences between the two taxa. Additionally, Sanders (1998) notes that the vertebrae of *A. africanus* Stw8 and *A. afarensis* are very similar to each other. However, since the australopithecine sample sizes in the present study are very small, they are likely prone to sampling error. The present results are most likely unreliable estimates of the species mean differences and the comparison with African ape mean differences is to be viewed with great caution. In conclusion then, the lumbar spine is probably not a very good diagnostic skeletal region to identify different australopithecine taxa.

Differences in vertebral shape between fossil hominins and modern hominoid taxa

Results from all three analyses indicate that there are significant differences in vertebral shape between the modern taxa and the fossils. Modern humans are closest in shape to *Homo ergaster* and then australopithecines. Fossil taxa are rather different in vertebral shape from great apes. *Pan* and *Pongo* turned out to be the great ape taxa closest in

shape to *A. africanus*. Differences in shape between australopithecines and modern humans are usually larger than differences in shape between the two African ape means. This should be viewed with some circumspection however, because of issues of sampling. The australopithecine taxa resemble each other the most. The separate analysis of *Homo ergaster* with full samples of modern taxa indicates that its lumbar vertebrae are very similar in shape to modern humans and very different from all great ape taxa.

The fact that the australopithecine lumbar vertebrae seem to resemble modern humans, *Pan* and *Pongo* (in this order) most has an interesting implication: since humans are predominantly adapted to bipedal walking and *Pan and Pongo* to varieties of arboreal locomotion. Thus these findings suggest that the australopithecine lumbar spine shows adaptations to both, bipedalism and some form of arboreal locomotion.

5.5.3 Differences in vertebral shape between *A. africanus*, *Pan, Pongo* and *Homo sapiens*

Previous analyses (2 to 4) indicate that the mean lumbar vertebral shape of *A. africanus* resembles modern humans and – to a lesser extent – *Pan* and *Pongo*. Differences in shape between these taxa were assessed and described in analysis 5. Previous studies by Cook (1983), Robinson (1972), Sanders (1998), and Schmid (1991) point out that both australopithecine taxa (*afarensis, africanus*) are distinctive from all modern hominoid taxa in that their lumbar vertebral bodies are relatively small. Results from this present study confirm these findings. Furthermore, the present analyses confirm that the costal and spinous processes are relatively longer in australopithecines when compared to modern taxa (Cook, 1983; Robinson, 1972; Sanders, 1998; Schmid, 1991).

The analysis of highly complex three-dimensional shapes such as the lumbar vertebrae with geometric morphometrics has the advantage that one can observe how various anatomical components co-vary independent of size. Although australopithecine lumbar vertebral bodies are relatively narrower (medio-laterally) and antero-posteriorly longer, the relative length of the vertebral bodies seems not to vary substantially between humans, *Pan, Pongo* and australopithecines once size is removed. This indicates that although australopithecine vertebrae might be relatively narrow (medio-laterally) and tall (antero-posteriorly), they are not especially long (cranio-caudally) (for easier

identification of vertebral body dimensions, refer to figure 1.3, p. 34). These findings somewhat contrast with the argument brought forward by Robinson (1972) and Sanders (1998) that the relatively taller lumbar vertebral bodies add to the higher degree of flexibility in the australopithecine lumbar spine, although this does depend on what exactly is meant by 'relative'. In the present study all such relations refer to the shape of the vertebrae after scaling to the same centroid size, whereas Robinson and Sanders related lumbar vertebral length (cranio-caudally) to vertebral width (medio-laterally).

A further discrepancy from some earlier studies (Shapiro, 1993a) was observed in the size and shape of lumbar vertebral pedicles. Shapiro assessed pedicle dimensions through "pedicle area" (medio-lateral pedicle width multiplied with cranio-caudal pedicle length and "pedicle shape (ratio of pedicle width to pedicle length) (Shapiro, 1993a). In the present study, once size was removed, the pedicles of *A. afarensis* and *A. africanus* Stw572, Stw431 did not appear to be exceptionally different from modern humans in relative length. In Sts 14, they seem to be relatively longer. However, morphing the vertebral shapes from the vertebral level of L4 to L5 indicates that in all australopithecine specimens available pedicle length decreases considerably (more so in Sts14 than in Stw431) and medio-lateral pedicle width increases (mores so in Sts14 than in Stw431). This is very similar to what is observed in modern humans (Shapiro, 1993a). Nevertheless, on average, australopithecine pedicles seem to be relatively narrower than modern human ones. The mixed results from the analysis of Sts14, especially the hyper-human increase in pedicle width in the last lumbar is probably due to the fact that the reconstruction of the last lumbar vertebra was heavily influenced by reference to *Homo sapiens* (Robinson, 1972). Increase in pedicle width in *Australopithecus* was probably more like that observed in Stw431 – which is more than that in great apes but somewhat less than that in humans. Results from the present study are similar to those reported by Sanders (1998).

Interestingly, comparisons of mean vertebral shapes of humans, *Pan*, *Pongo*, and australopithecines indicate a smaller relative size of the superior articular joints and facets of *A. africanus* than previously reported (Sanders, 1998). Compared to the great apes, the superior articular processes are relatively shorter (in particular when compared to *Pongo*) but they are clearly relatively longer than those of modern humans. Concerning the inferior articular processes, australopithecines have relatively longer inferior articular processes than any of the great apes but they are relatively shorter than

those of modern humans. The distribution of articular process length is therefore unique in *Australopithecus*, although it resembles modern humans most. The latter have short superior and long inferior articular processes whereas great apes have long superior and short inferior ones.

5.5.4 Differences in shape between *Homo ergaster* and *Homo sapiens*

Analysis 2 showed little difference in vertebral size and shape between *Homo sapiens* and *Homo ergaster*. Some differences in shape observed between the two *Homo* taxa are related to pathology in the *Homo ergaster* specimen (see later in this chapter) However results from analysis 5 also indicate that some differences in shape between the two *Homo* taxa resemble differences in shape between *Homo sapiens* and the australopithecines. Compared to modern humans *Homo ergaster* shows longer costal and spinous processes. Inferior articular processes are relatively shorter and superior ones are relatively longer in *Homo ergaster*. Nevertheless and having regard for issues of sampling, compared to *Australopithecus* and modern great apes, the distribution of articular process length appears more like that observed in *Homo sapiens* than in any of these taxa. These results match those from the previous study by Sanders (1998) and underpin the first reports on vertebral shape by Brown et al. (1985).

While this finding relates to a single representative (subadult, at that) of *Homo ergaster*, early *Homo* might have retained some aspects of ancestral vertebral morphology, which only disappeared in later *Homo* taxa. The vertebrae of specimen KNM-WT 15000 are not fully mature (Latimer and Ward, 1993) and show some pathological changes, hence the ratio of vertebral body size and vertebral processes could have changed into adulthood (as seen in modern humans) or might have been altered by disease.

5.5.5 The pathological shape of the *Homo ergaster* lumbar vertebrae

The comparison of the mean shape of immature modern human material with the mean of *Homo ergaster* vertebrae showed that the latter has pathologically altered lumbar vertebrae. The pathological alterations affect the whole vertebrae (body, arch, costal and articular processes, and the spinous process). The alterations in vertebral shape observed in the lumbar spine of KNM-WT 15000 are probably best explained by the presence of scoliosis (of relatively mild degree). The scoliotic vertebral column deviates laterally

from its normal mid-sagittal plane (Ortner and Putschar, 1985). In a scoliotic lumbar spine, the transverse processes are long, slender and pointed on the concave side. On the convex side they are plump and short (Ortner and Putschar, 1985). The roots of the transverse processes are deflected backwards on the convex side and forwards on the concave side of the curvature. Spinous processes tend to bend in the direction of the concavity of the curvature and vertebral bodies show lateral wedging. The spinous processes of the lumbar vertebrae of the *Homo ergaster* specimen are deflected to the left. The right costal processes are slightly deflected backwards whereas on the left side, they seem to be slightly deflected forwards. As mentioned before, the vertebral arches are twisted in the posterior view (see figure 5.21). A slight lateral wedging of the vertebral bodies noted exploring the landmark data has been confirmed to be present on pictures of the specimen published in Walker and Leakey (1993). All these features are in accordance with a scoliosis. A scrutiny of the lower thoracic vertebrae would clarify if there were signs of the compensatory curvature usually observed in scoliosis. Such double curvature allows the position of the head to be close to the mid-sagittal plane despite the lateral deviation of the vertebral column. Further, the ribs of the specimen KNM-WT 15000 should also be subjected to close scrutiny. Scoliosis tends to affect the shape of the ribs, which have to adapt their shape and curvature to the spinal deformity. Recently, Latimer and Ohman (2001) examined the postcranium of KNM-WT 15000 with regards to the pathological changes present. They confirm – among other pathological changes – the presence of the scoliosis, in combination with rib distortions and clavicular asymmetries. They consider some of the abnormalities acquired – among these the scoliosis – but also conclude that other observations are most consistent with an axial dysplaysia of congenital origin.

5.5.6 Assessing differences in patterns of vertebral size and shape variation along the lumbar spine between modern and fossil taxa

Previous studies of patterns of vertebral size and shape variation between modern hominoid taxa show that differences in locomotor repertoires influence the patterns of size and shape variation along the lumbar spine. Therefore, analysis 6 explored differences in patterns of vertebral size and shape variation between fossil and modern taxa. *A. afarensis* had to be excluded from this analysis because there were not enough vertebrae available.

The comparison of patterns of vertebral size variation between *Homo ergaster* and modern taxa revealed that *Homo ergaster* somewhat surprisingly lacks the increase in centroid size between L4 and L5 characteristic of humans (and absent in apes). This is observed, but to lesser degree in only 7% of the sample of modern humans available to this study.

The relatively erratic increases and decreases in vertebral size between L2 and L4 in Sts431 and Sts14 are likely to be artefacts caused by relatively poor conservation of the vertebral bodies of L2 and L3 in both specimens. Nevertheless, the pattern of metameric variation in size of *A. africanus* specimen Stw431 resembles that of the *Homo ergaster* specimen. In contrast Sts14 shows a more human-like pattern with a large increase in vertebral size observed between L4 and L5. The differences in patterns of size variation between Sts14 and Stw431 might be seen in relation to the reconstructions performed (irreversibly) on the original fossils of Sts14 by Robinson.

Previous comparisons of patterns of vertebral size variation between humans and great apes showed that differences between them are related to differences in load transmission through the lumbar spine and so to habitual trunk posture and locomotion. In humans, lumbar vertebral size increases cranio-caudally and considerably so between L4 and L5. This is because of the position of L5 in relation to the sacrum and the upright trunk and the cumulative load of body weight resting on it. Thus, body size as well as locomotion has a clear influence on the pattern of vertebral size variation. The assumption that *Homo ergaster* was a habitual biped and probably also an endurance runner like modern humans is well supported by morphological evidence (Bramble and Lieberman, 2004; Latimer and Ward, 1993; Wang et al., 2004). It is unclear therefore if the differences observed here represent sampling (this pattern is normal in 7% of modern humans), differences in body weight or load transmission (unlikely) or pathology.

In contrast to what has been observed in the comparison of patterns of vertebral size variation, the patterns of vertebral shape variation of both *Homo ergaster* and *A. africanus* resemble humans most and are very different from all great ape taxa. Compared to *Homo sapiens* the pattern *in Homo ergaster* is very similar, only small variations in magnitude of shape changes between consecutive vertebrae are observed and these are likely due to sampling error or the pathological condition of the *Homo*

ergaster specimen. In comparing metameric patterns shape variation of *A. africanus* with that of modern humans, differences in the magnitude of shape variation between successive vertebrae are observed. Thus large differences in shape occur between L1 and L2 as well as L4 and L5. In modern humans, the difference between L1 and L2 is small and large between L4 and L5.

The occurrence of a large jump in vertebral shape between L1 and L2 in *A. africanus* is interesting. This might indicate that australopithecine vertebral shape differs considerably between thoracic and lumbar regions. Other researchers have reported that the thoracic vertebrae of both, *A. afarensis* and *A. africanus* strongly resemble those of great apes (Robinson, 1972; Sanders, 1998; Schmid, 1991). This has been interpreted as an adaptation to the extensive shoulder muscles inserting into the thoracic spine. The extensive shoulder muscles in turn are seen as reflecting the adaptation to arboreal locomotion (climbing). To further clarify this issue the pattern of shape variation along the entire thoraco-lumbar spine of *Australopithecus* should be compared with those of apes and humans. If the assumption is true that the thoracic spine is adapted to climbing whereas the lumbar region is adapted to bipedal gait, the pattern of *A. africanus* should resemble great apes in the thoracic region and humans in the lumbar region.

In the comparison of patterns of vertebral shape variation between the modern hominoid taxa (see Chapter IV), it was shown that differences in patterns of shape variation are related to differences in locomotor repertoires. If these results are applied to the differences in patterns observed between humans and australopithecines, then it seems likely that the similarity in patterns of metameric shape variation along the lumbar spine between australopithecines and humans indicates some similarity in locomotion – namely bipedal gait. This would indicate that the australopithecine lumbar spine shows adaptations to a bipedal gait and that bipedalism was an important part of the australopithecine locomotor repertoire. The similarities in metameric shape variation patterns are most likely attributable to a habitual upright trunk posture. Thus, vertebral bodies and arches steadily increase in width and the distance between articular joint facets increases. Vertebral processes (costal and spinous) become shorter. All these shape variations along the lumbar spine have been described in modern humans in relation to the permanent upright trunk posture e.g. (Farfan, 1978; Odgers, 1933; Ortner and Putschar, 1985; Pal, 1989; Pal and Routal, 1987; Putz, 1981; Sanders, 1998; Schultz, 1961; Schultz and Straus, 1945; Shapiro, 1993b). The same shape

configurations have been previously described for *Australopithecus* (Robinson, 1972; Sanders, 1998) and they make a strong case that australopithecines show adaptation to upright trunk posture and presumably bipedal gait. In addition, the differences in vertebral shape between humans and australopithecines and the smaller similarities in australopithecine vertebral shape to *Pan* and *Pongo* likely indicate a mixed adaptation of the vertebral column to bipedal gait and arboreal climbing locomotion. Studies of the australopithecine post cranium e.g. pelvis, femur, foot anatomy, and overall body proportions indicate that the human and australopithecine bipedal gaits were rather different from each other and adaptations to arboreal locomotion are strongly present (Berge, 1994; Häusler and McHenry, 2004; Latimer, 1991; McHenry and Berger, 1998; Stern and Susman, 1983).).

5.6. Conclusions

5.6.1 Differences in vertebral shape between the australopithecine specimens

The analysis of single lumbar vertebral size and shape variation revealed that both australopithecine taxa included in the present study are most similar to each other. Nevertheless, some anatomical features (e.g. the funnel-shape of lumbar vertebral bodies, relatively long spinous process etc) seem to be more accentuated in *A. afarensis* when compared to *A. africanus*. If these findings are expressions of individual variation or if they are still valuable in the light of an extended sample of both *A. afarensis* and *A. africanus* specimens has to be seen when this sample is available. Due to the present small sample size, all results concerning differences in vertebral size and shape between *A. africanus* and *A. afarensis* are to be read with caution. Differences in shape between *A. africanus* specimens, especially between specimen Sts14 and all other specimens are best seen in the light of the human-like reconstruction of specimen Sts14. Sexual dimorphism in vertebral size may be present in *A. africanus* and if so this indicates (in accordance with results from Chapter III, intra-specific differences) sexual dimorphism of body weight.

5.6.2 Differences in vertebral shape between *Homo sapiens* and *Homo ergaster*

The *Homo ergaster* specimen KNM-WT 15000 has lumbar vertebrae which most resemble those of juvenile modern humans in vertebral size and shape, despite the fact

that this particular specimen shows signs of lumbar scoliosis. The pattern of metameric shape variation is very similar to that seen in modern humans whereas the pattern of metameric size variation is not so clearly modern. Also somewhat different from modern humans are the relative lengths of vertebral processes and relative sizes of the vertebral bodies of *Homo ergaster*. They resemble those of *Australopithecus* in their proportions. However, the overall shapes of the *Homo ergaster* vertebrae are clearly more *Homo sapiens*–like. Different proportions of vertebral bodies and vertebral processes could either be due to individual variation or the juvenile status of the *Homo ergaster* specimen. In general, however *Homo ergaster* seems to have had lumbar vertebrae that closely resemble those of modern humans. This would indicate the presence of an active lumbar lordosis and the ability for trunk torsion (flexion-extension-rotation motion) during locomotion. This would be consistent with *Homo ergaster* being capable of long distance walking and bipedal running.

5.6.3 Differences in vertebral size and shape between *Australopithecus* and modern hominoid taxa

The lumbar vertebrae of *Australopithecus* are smaller than those of *Gorilla* and *Homo sapiens* but clearly within the range of *Pan* and *Pongo*. Patterns of vertebral size variation resemble great apes in specimen *A. africanus* Stw431 but humans in Sts14 (especially between L4 and L5). However, the latter might be less human-like had the last lumbar not been reconstructed in a hyper-human style by Robinson. Therefore, the pattern displayed by Stw431 is probably somewhat more reliable.

The lumbar vertebrae of *Australopithecus* resemble modern humans most. Of all the great apes, *Pan* and *Pongo* are closest to them in vertebral shape. Differences in vertebral shape between humans and australopithecines have been identified by previous workers (Benade, 1990; Robinson, 1972; Sanders, 1998; Schmid, 1991; Shapiro, 1993a). Australopithecines have relatively smaller vertebral bodies and relatively long vertebral processes (spinous and costal) when compared to modern humans and great apes. The distribution of articular process lengths is also distinctively australopithecine: it is intermediate between the pattern of great apes (long superior, short inferior articular processes) and that of modern humans (short superior, long inferior ones). In contrast to the metameric pattern of vertebral size variation, that of shape variation resembles humans far more than those of great apes. The way shape

varies along the lumbar spine is in essence the same as in modern humans with the addition of a large difference in shape variation between L1 and L2.

The australopithecine vertebral size (resembling *Pongo* and *Pan* most) and the metameric pattern of vertebral size variation (resembling the great apes most) raise interesting considerations. Previous studies of intra- and inter-specific differences in vertebral size (Chapters III and IV) indicate that in quadrupedal and arboreal climbing hominoid taxa, vertebral size solely reflects differences in body weight (intra- and inter-specifically). Only in modern humans (fully specialized, relatively heavy weighted hominoids) is vertebral size also influenced by locomotor functions – specifically due to habitual trunk posture and the vertebral column loading pattern that goes with it. Based on the findings of the present study regarding vertebral size and patterns of size variation of australopithecines one would not identify them as habitually bipedal forms.

In the studies of Chapter IV which examined vertebral shape differences between extant taxa these differences principally reflected differences in locomotion. If australopithecines are no exception from this, then one can assume that the close similarity in vertebral shape and in patterns of metameric variation of shape between modern humans and australopithecines probably relates to bipedal gait. Likewise the differences in vertebral shape between *Homo* and *Australopithecus* probably reflect differences in the biomechanics of bipedalism and the more diverse locomotor repertoire of *Australopithecus*.

5.6.4 Relationships between vertebral size and shape variation between fossil and modern taxa and locomotor repertoires

From the study of other postcranial skeletal regions (e.g. feet, femur, pelvis, thorax, and upper limb) various workers conclude that the australopithecine bipedal gait differs from modern humans in biomechanics, energetic efficiency, distance, and speed (Aiello and Wells, 2002; Kramer, 1999; Kramer and Eck, 2000; Pontzer and Wrangham, 2004; Sellers et al., 2004; Wang and Crompton, 2004; Wang et al., 2004).

The most important differences between modern humans and australopithecines are believed to be the differences in body proportions since they have the most profound impact on the type of bipedalism possible (Bramble and Lieberman, 2004; Jungers,

1983; Wang and Crompton, 2004; Wang et al., 2004). Australopithecines resemble great apes most in body proportions. In relation to the vertebral column, the shape of the trunk is of greatest interest. Compared to great apes, humans have a more slender trunk with a barrel-shaped thorax and a waist between thorax and pelvis. The latter is narrower and shorter than that of great apes. The combination of short pelvis, barrel-shaped thorax, and relatively long lumbar spine (for a hominoid), allows for the counter-rotation of upper and lower limb in modern human bipedalism (via flexion-extension-rotation motion in the lumbar spine). This in turn supports the exchange of kinetic energy in connective tissue and bone architecture (ligaments, active lumbar lordosis) and provides the necessary balance and counter-action of momentum in running (Alexander, 1992; Bramble and Lieberman, 2004; Gracovetsky, 1986).
Australopithecines do not show modern human body proportions. Their pelvis, albeit short, is broader (Häusler, 2002). The thorax is funnel-shaped like in great apes and in combination with the broad pelvis does not add up to a trunk morphology with a waist and the capacity trunk torsion and counter rotation of the upper and lower limbs (Schmid, 1991; Wang and Crompton, 2004; Wang et al., 2004).

The closer resemblance of australopithecine body proportions and trunk morphology to those of great apes likely indicates less mobility in the australopithecine trunk. This is to be seen in relation to adaptations to arboreal locomotor modes (climbing). Non-human hominoids are among the largest forms regularly engaging in arboreal locomotion. In relation to their large body weight, their climbing locomotion favours a rigid trunk with limited flexion and extension in the sagittal plane and minimal lateral bending and rotation in the trunk. This is to reduce shear and torque stresses in the vertebral column during climbing (Hunt, 1991b; Ward, 1993b). If mobility in the australopithecine trunk is indeed less than that in modern humans (especially in relation to lateral bending and torsion in the trunk), the biomechanics of their bipedal gait would have differed from that of modern humans.

5.6.5. The issue of lumbar spine flexibility in australopithecines

The trunk morphology of australopithecines suggests reduced trunk torsion and potentially less lateral flexibility than modern humans. Nevertheless, Sanders (1998) considers the length of the australopithecine lumbar spine (considered by him to comprise six lumbars) and the relatively long australopithecine lumbar vertebral bodies

as too long and too flexible to allow successful climbing locomotion as observed in African great apes. There is a conflict between the relatively inert trunk morphology outlined here and by Biegert and Maurer (1972) and Schmid (1991) and the supposedly very flexible lumbar spine reported for *Australopithecus*. Nevertheless, the australopithecine lumbar vertebral spine is probably not longer or more flexible than that of modern humans: First, the suggested modal number of six lumbars for australopithecines is debatable (Häusler et al., 2002) and in any case the number of vertebrae is only partially responsible for total length of the lumbar spine. Second, the results from the present study indicate that vertebral bodies of australopithecines are not clearly relatively longer than those of other hominoids.

Habitual bipedalism in relation to upright trunk posture ultimately causes the formation of a lumbar lordosis. Therefore, a lumbar lordosis is present in the spine of Japanese macaques (*Macaca fuscata*) – natural terrestrial quadrupeds - which have been trained to walk bipedally on regular basis (Hayama et al., 1992) or in (artificially) biped Wistar rats (Cassidy, 1988). The main components involved in producing the lumbar lordosis are the intervertebral discs, which become posteriorly wedge shaped. The lumbar lordosis forms due to the influence of gravity but can function as a shock absorber. Lumbar lordosis plays a role in relation to its effects on the ability for trunk torsion. It controls pelvic displacement during bipedal walking and running and assists in the exchange of potential and kinetic energy. If australopithecines did have a less mobile trunk, one would expect that the lumbar lordosis observed in the australopithecines while acting as a thrust damper was not adapted to the highly distinctive flexion-extension-rotation motion seen in modern humans.

In relation to bipedal walking in trained Japanese macaques another interesting observation has been made: the size of lumbar vertebral bodies of macaques is considerably smaller in relation to their body weight when compared with hominoid primates (Nakatsukasa and Hirose, 2003; Schultz, 1933; Schultz, 1953). Yet when trained to walk on two legs for considerable amounts of time daily and over long periods, they do not have problems in supporting their body weight on substantially relatively smaller vertebral bodies than modern humans. This would indicate that australopithecines could have been functional bipeds despite their small vertebral bodies. One could argue that modern human vertebral bodies have become larger not for walking but as an adaptation to running (high peak loads impacting on the lumbar spine

and necessity to resist large momentum) and increase in body weight. The small vertebral bodies of australopithecines could therefore indicate that their bipedal gait did not show specializations for running and presumably also long distance running.

If arboreal locomotion played an important role in the australopithecine locomotor repertoire (postcranial adaptations of upper limb, thoracic spine, and toe phalanges indicate this), then a somewhat less flexible lumbar spine would be favourable. If the scenario of a somewhat less flexible lumbar spine than humans is assumed for australopithecines, the differences in vertebral shape between modern humans and *A. africanus* and *A. afarensis* should be seen in relation to adaptation to spine stabilization against lateral bending and torsion. Thus, the relatively longer than human superior articular processes of australopithecines could play a role in lateral bending restriction in that this joint might have interlocked more tightly than in modern humans (but probably not as extremely as is seen in the great apes). Alternatively, one could see the long superior articular processes as a plesiomorphic hominoid feature somewhat reduced in australopithecines and much more so in modern humans. It is the inferior articular processes of australopithecines, which allows more flexion-extension motion (sagittal plane) in *Australopithecus* than in great apes. In addition, the more horizontal orientation of the spinous process would allow increased flexion-extension motion of the australopithecine lumbar spine in comparison to great ape taxa. It should be borne in mind, however that flexion and extension of the lumbar spine require less restriction during climbing in large primates than does the lateral motion of the lumbar spine which can result in torsion stress (Boszczyk et al., 2001; Hunt, 1991b).

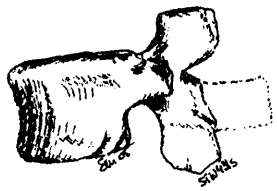
It has been suggested previously by Sanders (1998) and again by Schmid (1991) that the relatively longer costal processes of *Australopithecus* may be an indicator of better stabilization of the lateral motion of the trunk. This would fit well with the possibility that the australopithecine spine is probably more mobile than that of great apes but less so than that of modern humans. The longer costal processes provide a longer lever arm for the *Quadratus lumborum* which acts to stabilize the trunk during climbing in apes (Slijper, 1946). According to Häusler (2001), these muscles probably function in australopithecines in a more similar fashion to that of modern apes to stabilise the trunk during climbing.

The fact that the australopithecine lumbar spine is nearly as similar to that of *Pongo* as it is to *Pan* serves to corroborate the opinion voiced by various researchers that the African ape model is probably not adequate for early hominin locomotor repertoires and bipedal gait (Crompton et al., 1999; Oxnard, 1983). Clearly the locomotor repertoire of *Pongo* is equally relevant in such studies. It is noteworthy that Schmid (1991) concludes that arboreal locomotion resembling that of Asian apes would probably be a relatively good comparative model for the arboreal locomotor repertoire of *A. afarensis*. Orang-utans utilize a more erect body posture during voluntary bipedalism. And although unassisted bipedal gait is less common in wild orang-utans than in the African great apes, they display much more extended hip and knee posture in their almost entirely arboreal behaviour (Crompton et al., 1999; Thorpe and Crompton, 2005). These observations, in combination with the pelvic and hindlimb morphology of the australopithecines would indicate that their arboreal locomotion probably contained a large amount of erect posture not only during bipedal gait but also during climbing as observed in living orang-utans (Wang and Crompton, 2004).

5.6.6 Summary

The comparison of fossil hominin lumbar vertebral size and shape variation with that of modern hominoid taxa firstly confirms the close similarity of *Homo ergaster* and *Homo sapiens* lumbar vertebrae. They also confirm the similarity of *Homo sapiens* and *Australopithecus* lumbar spines. The results corroborate previously described differences in vertebral shape between fossil and modern taxa. Additionally, this study finds that of all the modern great ape taxa, *Pan* and *Pongo* are almost equidistant in shape from *A. africanus* and *A. afarensis*.

In relation to locomotor repertoires these findings indicate an extensive mix of adaptations to bipedal gait and to arboreal locomotion in the australopithecine lumbar spine. In combination with the other parts of the postcranium, the lumbar vertebral column of australopithecines shows intermediate capacity for flexion-extension motion in the sagittal plane and stabilization against spinal torsion (trunk torsion and to a lesser extent lateral bending). The biomechanics of australopithecine gait were likely different from those observed in modern humans.



CHAPTER VI, CONCLUSIONS

The work of this thesis has focussed on variation in the lumbar spine of living and fossil hominoids. The thesis is presented in six chapters, the first two of which provide the background to this study in terms of the issues at hand and materials and methods used. The next three chapters are summarised below, they examine patterns of intra and inter-specific variation in lumbar vertebral size and shape. This is the final chapter which aims to bring together the findings, draw general conclusions, suggests analyses for future fossil vertebral findings, and points the direction to future work.

6.1. Summary of results

6.1.2 Chapter III (intra-specific size and shape variation, modern hominoids)

This study examined intra-specific lumbar vertebral size and shape variation within the recent hominoid taxa *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*. Intra-specific differences were explored and interpreted in relation to intra-specific differences in overall body weight (sexual dimorphism) and locomotion.

Aims of study

They included

- The confirmation or otherwise of the presence of intra-specific differences in vertebral size and shape within each taxon
- The investigation of relationships between dimorphism in vertebral size and shape with sexual dimorphism in body weight and (sexual) differences in locomotion
- The investigation of the extent to which patterns of inter-segmental shape variation along the lumbar spine differ between the sexes of the four hominoid taxa in the study and the relationship of these to sexual dimorphism in body weight and (sexual) differences in locomotion
- How sexual dimorphism in vertebral size and shape is established throughout postnatal ontogeny

Results

With regard to the first aim, the presence of sexual dimorphism in vertebral size was confirmed to be significant in all four taxa. Sexual dimorphism in vertebral shape, on the other hand, was confirmed only in the largest apes *Gorilla*, probably *Pongo* (small sample size), and *Homo sapiens*. The differences in vertebral shape between the sexes in *Pan* were non-significant. Humans are characterized by larger differences in vertebral shape than size between the sexes. This despite the fact that the smallest ♂/♀ body weight ratio is observed in modern humans. In contrast, in the large sized apes, vertebral size dimorphism exceeds vertebral shape dimorphism.

In examining how sexual dimorphism in vertebral size and shape between the sexes of large apes and *Homo sapiens* relates to sexual dimorphism in body weight the following findings were made: Sexual dimorphism in body weight impacts considerably on differences in vertebral size between the sexes of the large apes *Gorilla* and *Pongo*. In modern humans, habitual body posture and the ability to run long distances have probably a higher influence on vertebral size than does body weight (sexual dimorphism is the smallest in humans). Metameric patterns of vertebral size variation along the lumbar spine did not differ between the sexes of any of the taxa, including *Homo sapiens*. Patterns of vertebral shape variation along the lumbar spine do not vary between the great ape taxa. In contrast, male and female *Homo sapiens* show different patterns. These are most different at comparison level 4 (L5), indicating that the last lumbar vertebra is different in shape between the sexes.

Results from the analysis of the postnatal development of sexual dimorphism indicate likely differences in patterns of postnatal ontogeny of vertebral size and shape between great apes and *Homo sapiens*. These findings are, however, tentative given the poor subadult samples of *Homo* and *Pongo*.

Conclusions

Results from the study of intra-specific differences (sexual dimorphism) in vertebral size and shape of modern great ape taxa indicate a strong relationship between sexual size dimorphism in body weight and vertebral size but a less pronounced relationship between weight dimorphism and vertebral shape. In apes, sexual dimorphism in locomotion (differences in frequencies of locomotor modes) does not have an impact on vertebral size and shape (Cant, 1987a; Doran and Hunt, 1994; Remis, 1995). Sexually

dimorphic differences in locomotor kinematics (Isler, 2005; Isler and Thorpe, 2003) do not have a relationship with differences in vertebral size and shape either. In humans, vertebral size dimorphism is likely not only related to body weight dimorphism as previously observed in great ape taxa but also to locomotion (running) and habitual body posture (upright). In contrast to apes, sexual differences in vertebral shape not only relate to body weight dimorphism, but also to sexual dimorphism in pelvic and sacral morphology. In turn these obstetrically driven dimorphisms likely impact on vertebral dimorphism through differences between males and females in their kinetics and kinematics of bipedal locomotion.

6.1.3 Chapter IV (inter-specific size and shape variation, modern hominoids)

This study examined inter-specific variation in lumbar vertebral morphology between recent hominoid taxa and considered the extent to which this variation is influenced by inter-specific differences in body weight, locomotor repertoires and phylogenetic history.

Aims of study

They include

- The confirmation of differences in lumbar vertebral size and shape between *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*
- The investigation of relationships between these differences in vertebral size and shape and inter-specific differences in body weight, locomotor repertoire, and phylogenetic history
- The investigation of the extent to which patterns of inter-segmental size and shape variation along the lumbar spine differ between the four hominoid taxa in the study
- The preliminary investigation of how these differences are established throughout postnatal ontogeny

Results

Addressing the first aim, the exploration of inter-specific differences in vertebral size and shape between the four hominoid taxa showed that there are significant differences in vertebral size and shape between the taxa. Nonetheless, there are some exceptions to this: Differences in lumbar vertebral size between *Homo sapiens* and *Gorilla* and

between *Pan* and *Pongo* are non-significant. Patterns of vertebral size variation along the lumbar spine vary between humans and all great apes but not between the great apes. Lumbar vertebral shape, on the other hand, differs highly significantly between all four taxa with modern humans being the most different, followed by *Pongo* and the African apes. *Pongo* and *Homo sapiens* both manifest patterns of metameric shape variation which are considerably different from African apes and each other.

The investigation of relationships between inter-specific differences in vertebral size and shape and inter-specific differences in body weight, locomotor repertoires, and phylogeny (second aim) showed that locomotor repertoires have a strong relationship with vertebral shape and body weight with vertebral size. The exception is *Homo sapiens* whose lumbar vertebrae are larger than would be expected for a hominoid of their weight because of bipedal gait. Phylogeny is not reflected in vertebral size or shape variation.

Differences in locomotor repertoires are also reflected in differences in patterns of inter-segmental shape variation along the lumbar spine. Additionally humans have characteristic patterns of metameric size variation, likely due to adaptations to bipedal gait and spinal mobility.

The results from this study also show that characteristics of the three different metameric patterns of size and shape variation (African apes, Asian ape, *Homo sapiens*) are already established in infant and juvenile specimens. Nonetheless, differences in patterns are smaller between immature Asian and African apes than between adult specimens.

Conclusions

The significant relationship between inter-specific differences in locomotor repertoires and both single lumbar vertebral shape and patterns of vertebral shape variation between all modern taxa indicates that the lumbar spine is of value in investigating locomotion in fossil taxa. Importantly, the inter-specific differences in the shapes of lumbar vertebrae are not much influenced by differences in body weight. This is of considerable importance for the study of fossil forms. The results suggest it is possible to obtain reliable insights into the locomotion of fossils from the shape and pattern of metameric

variation of its lumbar vertebrae. Even isolated vertebrae are informative, which is very attractive in the investigation of the often fragmentary fossil record.

6.1.4 Chapter V (fossil shape variation)

This study explored inter-specific differences in lumbar vertebral shape between fossil hominine taxa and the modern hominoid taxa (*Pan, Gorilla, Pongo*, and *Homo sapiens*). Differences in vertebral shape between the fossil hominins and modern hominoid taxa were then discussed in relation to the preceding review (Chapter I, introduction) and in relation to the results of the studies from Chapters III and IV – therefore in the context of known and hypothesised differences in locomotor functions between fossil and modern taxa.

Aims of study

They include

- The assessment of lumbar vertebral size and shape variability of *Australopithecus* relative to that found in modern taxa
- The assessment of the differences in size and shape between the fossil hominin taxa *A. africanus*, *A. afarensis,* and *Homo ergaster* and the modern hominoid taxa of previous studies (Chapters III and IV)
- The investigation of the extent to which differences in size and shape between fossil taxa and between fossil and modern taxa relate to currently held views on their locomotor repertoires

Results

With regard to the first aim, results of the fossil study showed first, that australopithecine taxa (*A. afarensis* and *A. africanus*) are quite similar to each other in vertebral size and shape. The only available *A. afarensis* vertebra is small but similar to the *A. africanus* specimens in shape. This said, certain characteristic features of australopithecines (e.g. 'funnelled' body) are more pronounced in *A. afarensis*. To what extent this is due to individual variation or inter-species variation cannot be decided here.

The comparison of vertebral size and shape between modern hominoid taxa and fossil hominins (*Australopithecus*, *Homo ergaster*) indicated that *Homo ergaster* (a juvenile

specimen) is not different in vertebral size from juvenile *Homo sapiens* (and *Gorilla*). Nonetheless, the pattern of vertebral size variation along the lumbar spine of *Homo ergaster* resembles the great ape means more than that of the modern human mean because there is a decline in vertebral size between L4 and L5. Such a decline but to lesser degree is found in 7% of the modern human sample. The australopithecine lumbar vertebrae are quite similar in size to those of *Pan* and *Pongo*. Their pattern of vertebral size variation (*A. africanus* only) resembles that of great apes while Sts14 shows a more human pattern, which is highly likely due to errors of reconstruction of the last lumbar. If *A. africanus* Sts14 is a female and the other three specimens in the sample male, vertebral size dimorphism is intermediate in degree between *Gorilla* and *Pongo* (larger size dimorphism) and *Homo sapiens* and *Pan* (smaller size dimorphism).

Lumbar vertebral shape as well as the metameric pattern of vertebral shape variation of *Homo ergaster* resembles *Homo sapiens* most and is very different from all great ape taxa. Both australopithecine taxa resemble modern humans most. However, they show a combination of morphological features which distinguish them clearly from humans. This combination of features is unique to australopithecines and consists of relatively long vertebral processes (costal, spinous) and small vertebral bodies. The pattern of metameric shape variation of *A africanus* resembles humans most. Of the apes, australopithecine vertebral shape is most similar to *Pan* and nearly as similar to *Pongo*.

Conclusions

From the results of the fossil study, the following can be concluded. First, the australopithecine species are very similar. Second, the close resemblance of vertebral size and shape between modern humans and *Homo ergaster* likely indicates adaptations to bipedal gait and presumably running in *Homo ergaster* very similar to that of modern humans. Third, the close resemblance of australopithecine and *Homo sapiens* lumbar vertebral morphology shows that australopithecines had a lumbar spine adapted to bipedal gait. However, their similarities to both *Pan* and *Pongo* probably reflect adaptations to arboreal locomotion. Differences in vertebral morphology between humans and australopithecines may indicate a degree of spinal flexibility intermediate between that of modern humans and great apes.

6.2. Conclusions

The present study concludes by placing its findings in the context of some broader issues concerning the evolution of the hominoid lumbar spine.

6.2.1 How does the interpretation of the australopithecine lumbar spine morphology compare with results from the studies of other post cranial regions?

As discussed in Chapter I, there is a growing consensus that the australopithecine locomotor repertoire partially consisted of arboreal locomotion and partially of a form of bipedal gait characterized by full leg extension (Häusler, 2002; Stern et al., 1984; Wang and Crompton, 2004; Zihlman and Hunter, 1972) – although some disagree – (Lovejoy, 1974; Lovejoy, 2005; Ohman et al., 1997). Thus, the postcranium of australopithecines shows a combination of adaptations to both bipedal walking and arboreal locomotion. This mix of characters is seen in varying degrees in different anatomical structures depending on their role in locomotion. It is therefore no surprise that adaptations of the australopithecine postcranium to bipedal gait are foremost observed in the lower limb. Adaptations to arboreal locomotion are predominantly seen in the thorax and upper limb. The australopithecine vertebral column is no exception in that it shows adaptations to both bipedal gait as well as arboreal locomotion. Thus, the thoracic spine seems to resemble those of great apes (Gommery, 1997; Sanders, 1998; Schmid, 1991) whereas the lumbar spine resembles that of modern humans.

The findings of the present study agree with studies of other parts of the australopithecine postcranium: in general the lumbar spine of australopithecines resembles modern humans and is different from all great apes. It shows adaptations to bipedal gait but also a combination of unique australopithecine characters probably related to arboreal locomotion and the australopithecine bipedal gait which likely differed from that of modern humans.

6.2.2 How do the results of the present study relate to the evolution of the hominoid vertebral column?

In Chapter I, it was noted that all hominoids differ from cercopithecoids in that they have a shortened spine. This shorter spine results from a reduction of the length of the lumbar vertebral bodies as well as a reduction of the number of lumbar segments

(Schultz, 1961; Schultz and Straus, 1945). Significant differences between the cercopithecoids and all hominoids are also seen in the length of the sacrum, the shape of the trunk, the shape and length of the pelvis and the orientation of the scapula and shoulder-joints. These differences, leading to the typical ape morphology, arose throughout the Miocene. The Miocene is considered a relatively long geological epoch, spanning 19 myr, from approximately 24 myr BP to about 5 myr BP (Liem et al., 2001) The primate fossil record across this time span is not without gaps but adequate to confirm the emergence and radiation of ape-like primates during this epoch.

Miocene hominoids display a morphological and bio-geographical diversity that far exceeded that of the living apes and to date at least 30 genera have been identified (Ward et al., 1997). It is highly likely that out of this multitude, the ancestors of modern apes and hominins arose. Throughout the Miocene, the distribution of apes diminished and there were fewer taxa in the later than in the early stage (Andrews, 1981). Furthermore, towards the later Miocene, hominoids became more specialized for forelimb dominated climbing locomotion. Later representatives have a locomotor repertoire more similar, albeit not identical, to that of modern apes (Gebo et al., 1997; Gebo, 1993; Rose, 1993; Ward, 1997).

The early Miocene apes, such as *Pliopithecus vindobonensis* (Zapfe, 1960), did not differ much from present day cercopitheocoids in their morphology (Biegert and Maurer, 1972). Another well-known family of early Miocene apes, the Proconsulidae, known from several sites in Kenya and Uganda, is not only represented by skulls but also postcranial material. Therefore we know that they had a slender, long trunk and their spine was long and consisted of six or seven lumbar elements (Ward, 1993b). The proconsulid postcranium (in contrast to the skull), is hardly distinguishable from that of other early Miocene apes such as *Afropithecus*, *Turkanapithecus*, and *Kenyapithecus* (Ward, 1997). Ward therefore suggested that this morphology reflects the primitive hominoid condition. Adaptations in the elbow joint and the skeletons of the hand and foot probably made them quite apt climbers. They seem to have been predominantly arboreal animals and their locomotor repertoire most likely consisted of a combination of arboreal quadrupedalism, climbing, and suspensory activities (Rose, 1993; Ward, 1997). The lack of a tail further sets Proconsulidae apart from most cercopithecoids This absence of a tail persisted throughout all subsequent hominoid taxa (Ward, 1990; Ward, 1993a; Ward, 1997).

Only the later Miocene apes had a broad torso and a short spine (Biegert and Maurer, 1972; Schultz, 1960). It is therefore possible that the trend to a broad thorax and a shortened spine occurred by several different lineages of Anthropoidea, among them are the ancestors of modern Hominoidea, but also some Ceboidea which lead to *Ateles* (Ward, 1997). In terms of preservation, the late Miocene ape postcranium is best represented by *Oreopithecus bambolii*, a European ape from Italian locations (Hürzeler, 1958). *Oreopithecus* is distinguished from other hominoids by strongly divergent tooth and skull morphology, which ignited a large debate about its taxonomy. For a review see Harrisons and Rook (1997). However, *Oreopithecus*' closest fossil relative is probably *Dryopithecus* and, based on the postcranium, it has close affinities with modern ape taxa, which clearly classifies it as a hominoid (Harrison and Rook, 1997).

Schultz conducted a thorough comparison of the relatively complete *Oreopithecus* postcranial material with cercopithecoids as well as African and Asian apes (Schultz, 1960). *Oreopithecus* had a broad thorax as seen in modern apes. Its lumbar spine contained five vertebrae. Its sacrum was broad but not made up of as many vertebrae (five) as in apes (which have usually six to seven). However, the sacrum contains more vertebrae than in Cercopithecoidea (usually three to four), thus the sacralization of some lumbar vertebrae (as seen in all modern hominoids) had already taken place. Further, the pelvis of *Oreopithecus* was broad (supporting the claim of a broad trunk) but its iliac blades were not as extremely elongated and posteriorly rotated as observed in modern apes. Schultz describes their length as

„... nicht so stark verlängert wie bei allen rezenten Menschenaffen, sondern stehen in dieser Hinsicht nahe den Ceropitheciden und den Menschen"

„...not as extensively elongated as observed in all modern apes but in this aspect resembling more the cercopithecoids and humans" Schultz (1960)

Schultz and later Biegert and Maurer (1972) also observed the absence of an external tail, and noted that the body proportions resemble modern apes: *Oreopithecus* had short legs, due to short femora, and, based on humerus length, relatively long arms. The body proportions seem to resemble *Gorilla* the most, which of all living hominoids (except humans) has the relatively shortest arms. This motivated Schultz to interpret *Oreopithecus* as a general climber, with a relatively long lumbar spine and without the

specialized limb proportions of living apes adapted to extensive hanging-climbing behaviour such as it is seen in *Hylobates* or *Pongo*. However, according to some workers the *Oreopithecus* postcranium, in particular the pelvis, seem to show adaptations to bipedalism e.g. (Moyà-Solà and Köhler, 1997; Rook et al., 1999). Nevertheless, the same authors recently presented a study of the bony labyrinth (inner ear) which seems to indicate that *Oreopithecus* shows a positional repertoire and locomotor modes resembling those of modern great apes more than those of cercopithecoids and different from modern humans (Rook et al., 2004). The ongoing debate about *Oreopithecus*' locomotor repertoire apart, there seems to be general consent, that, including later taxa, Miocene apes express none of the quite distinctive adaptations to specialized modern ape locomotor patterns such as knuckle-walking or advanced brachiation and suspensory hanging-climbing (Rose, 1993), yet they all were highly likely rather arboreal than ground dwelling forms.

From the trend towards more specialized hanging-climbing locomotor patterns and short broad trunk and vertebral column throughout the Miocene, it can be hypothesized that the common ancestor of modern apes and the hominins probably still had a rather long lumbar spine and that its pelvis probably did not show the extensively elongated iliac blades of the modern apes. Figure 6.1 illustrates how the shape of the trunk, length of the lumbar spine, length and shape of the sacrum, and the shape of the pelvis could have transformed from a hypothetical Miocene ancestor towards the configurations observed in the modern great apes, modern *Homo sapiens*, and *Australopithecus*. After the split of the lineages leading towards modern chimpanzees and the hominins, chimpanzee evolution (and *Gorilla* evolution, in parallel if the currently dominant view from molecular phylogeny is correct) was characterized by further shortening of the lumbar spine (see figure 6.1B). This was achieved by the sacralization of further vertebrae (lumbar and caudal ones). It is highly likely that at the same time, the elongation of the iliac blades took place in the chimpanzee (and independently, *Gorilla*) ancestor (as discussed in Chapter I, the section about the number of lumbar vertebrae in Hominoidea, pp. 72-75).

In contrast, in the lineage (or lineages) leading towards australopithecines and modern humans, the lumbar spine conserved its five lumbar vertebrae and the pelvis shortened further from the ancestral condition (figure 6.1D). Later, in the lineage leading towards modern humans, the lumbar spine became more robust and more flexible. In addition,

the iliac blades became more anteriorly rotated (figure 6.1C). Lovejoy et al. (2000) show that the anterior rotation of the iliac blades could have been achieved by relatively small shifts in Hox gene expressions.

The Miocene common ancestor of modern apes and humans in figure 6.1 was made using a drawing of a chimpanzee pelvis which has been distorted (shortened and slightly narrowed), the lumbar spine and sacrum of a gibbon and the distorted (narrower) thorax of a chimpanzee. All drawings were taken from an illustration by Schultz (1950a), p. 438, comparing the trunk and pelvis of a macaque, a gibbon, a chimpanzee and a modern human. Schultz already had scaled the drawings of the four specimens to the same height to be able to make comparisons. The pelvic shape of *Australopithecus* is adjusted to resemble the reconstructions of australopithecine pelvic morphology according to Häusler (2001). Figure 6.1 is not meant to reconstruct the body proportions of either Australopithecines or the Miocene common ancestor of modern apes and hominins precisely but to give an impression of how transformations could have occurred from the common cercopithecoid-hominoid ancestor to the common ancestor of all hominoids and from there to modern apes, humans and australopithecines. Potentially, proportions could have transformed from those of australopithecines towards modern human proportions instead of the direct line implied by the arrow leading from the common Miocene ancestor towards modern humans (C, figure 6.1). However, since the phylogenetic relationships between Miocene apes, australopithecines, and modern humans are not resolved, this link has not been drawn in figure 6.1.

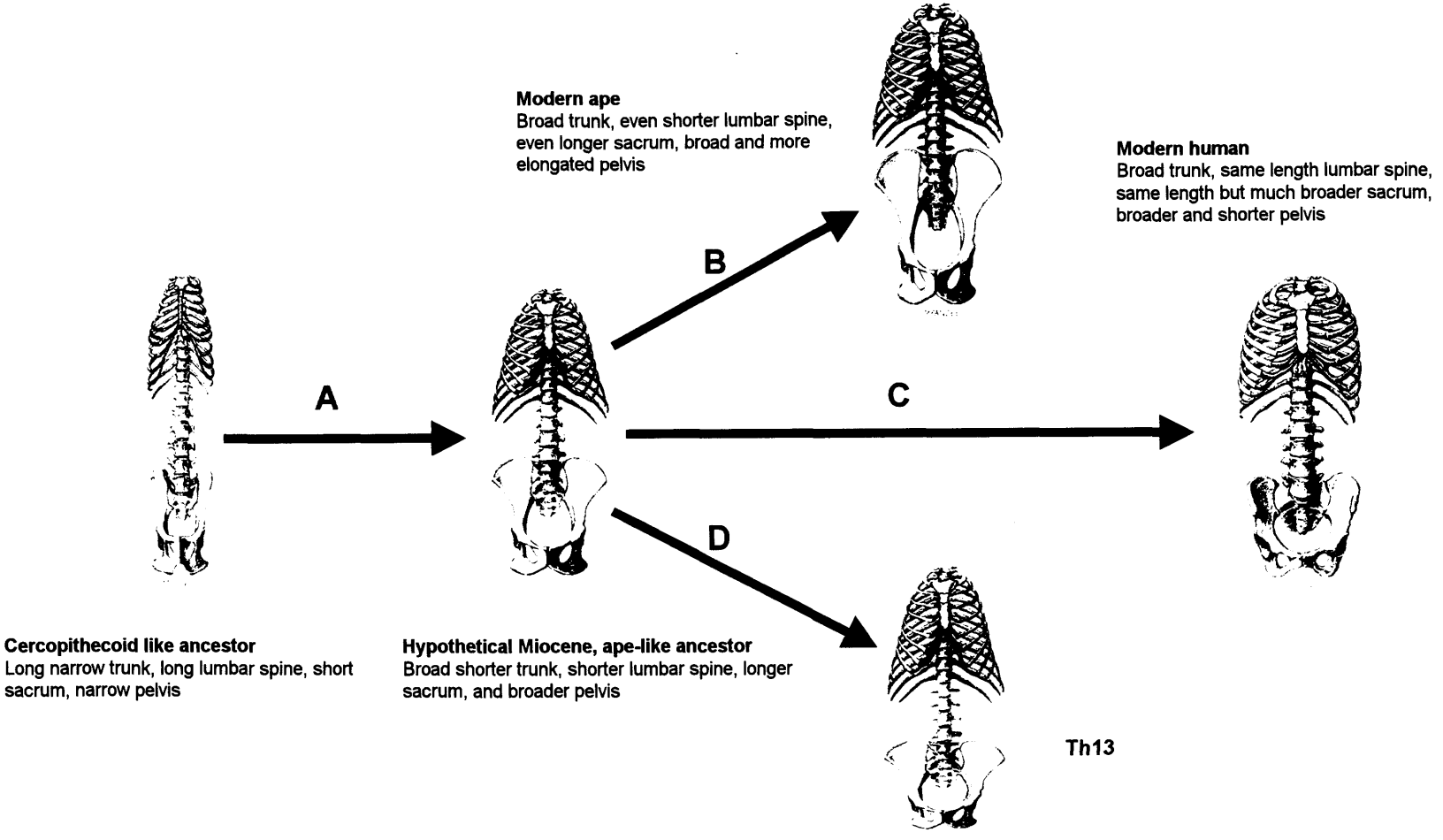


Figure 6.1 Hypothetical hominoid spine and pelvic shape radiation. **(A)** towards a Miocene common ancestor of modern hominoids and *Australopithecus*, **(B)** shape variation occurring at the split of the lineages towards great Asian apes, towards *Gorilla*, and again at the split towards *Panina* **(C)** shape variation occurring from Miocene ancestor towards *Homo sapiens* **(D)** shape variation from Miocene ancestor towards *Australopithecus*. Adapted and redrawn from Schultz (1950a), p. 438. Figures are not proportionally scaled

Albeit, the model of trunk and spine morphology radiation hypothesized in figure 6.1 poses a problem in that it makes it necessary to postulate that the elongation of the iliac blades and shortening of the lumbar spine occurred more than once in the hominid lineage, since the ancestral forms of *Gorilla* split from the chimpanzee-human-lineage at an earlier stage (supported by molecular data), yet *Gorilla* and *Pan* morphologies are remarkably similar. *Gorilla*, and in *Pan* parallel, apparently became highly specialized towards an arboreal locomotor repertoire which – probably at a later stage – included ground dwelling. This sets the African ape locomotor repertoire apart from that of the Asian great ape taxon, *Pongo*. In the lineage towards *Australopithecus* arboreal locomotion patterns was combined with bipedal gait. In the lineage towards modern humans, arboreality disappeared. It has been postulated that the disappearance of adaptations to arboreal locomotion should be seen in relation to the acquisition of adaptations to running (Bramble and Lieberman, 2004). This would indicate that adaptations to bipedal running as seen in modern humans are not yet present in the australopithecine taxa.

6.2.3 Does the lumbar spine of australopithecines show adaptations to bipedal endurance running?

The results from the present study show the australopithecine lumbar spine to express human-like features as well as more ape-like ones and unique australopithecine features. They underline the mosaic nature of australopithecine postcranial morphology already shown in various other postcranial elements of australopithecines (feet, femur, pelvis etc). The vertebral column is informative in terms of being diagnostic for specific locomotor and postural adaptations in mammals generally, and australopithecines are no exception from this. The results from the present study corroborate the assumption that a) australopithecines show adaptations to bipedal gait and b) they also show extensive adaptations to arboreal locomotion. As has been shown in previous studies, the pelvis and hindlimbs clearly show extensive adaptations to bipedal gait. On the other hand, overall body proportions, thorax shape and upper limb morphology are better seen in relation to adaptations to arboreal locomotion. Of course this does not mean that australopithecines are chimaeras that are perfectly adapted to climbing in their upper limb and body and to bipedalism in the lower half of their body. Rather, if one assumes that they stem from an ancestral form which relied predominantly on arboreal locomotion, one can also claim that australopithecines are predominantly adapted to

arboreal climbing – with the addition of a few but important adaptations to bipedal gait (see previous section). In this, they would resemble African great apes which are predominantly adapted to arboreal climbing but at the same time are very capable of terrestrial quadrupedal gait and show some key adaptations to this form of locomotion (adaptations to knuckle-walking). Depending on species, terrestrial locomotion accounts for a considerable percentage of the locomotor repertoire in African great apes. Compared to non-hominoid primates, the quadrupedal gait of African great apes is less energetically efficient (Pontzer and Wrangham, 2004) but this does not prevent the great apes engaging extensively in this particular locomotor mode.

A similar scenario could be created for australopithecines. In this case, the predominantly arboreal locomotor adaptations are combined with key adaptations in specific parts of the postcranium which allow a reasonably efficient bipedal gait. Although frequent bipedal gait requires adaptations which have a large impact on postcranial morphology (in particular in the pelvis and lower limb), these adaptations could have been due to a few small but substantial changes in the expression of genes (e.g. Hox genes) which result in different morphology (Lovejoy et al., 2000). The resulting australopithecine bipedal gait was likely a good compromise between arboreal and bipedal locomotion. The vertebral column is crucial in this in two different aspects: First, it connects upper and hindlimbs and it is part of the mechanism that propels animals forward. It also supports body weight. As stressed before, the lumbar spine of mammals reflects locomotor repertoires. The australopithecine lumbar vertebrae resemble modern humans the most – in relation to bipedal gait this is hardly surprising. However, in all great ape taxa, there are clear adaptations visible in the lumbar spine which set them apart from modern humans and are seen in relation to arboreal locomotion. Thus, lumbar vertebral features such as the shapes of the lumbar vertebral bodies and the posterior angulation of the inferior articular processes are relatively easily achieved in habitual bipedal gait – because there is a strong mechanical component which shapes these features in combination with gravitational forces. Thus, Hayama et al. (1992) show that bipedal gait in primates results in a mandatory lumbar lordosis as the example of Japanese macaques, trained to habitually walk bipedally shows to perfection.

In contrast to *Australopithecus*, *Homo sapiens* shows some distinct differences in body proportions, trunk shape, and lumbar spine morphology which set them apart from the

australopithecines. These adaptations are probably best seen as adaptations to long distance running (Bramble and Lieberman, 2004; Wang et al., 2004). Among these are a larger flexibility of the human lumbar spine – expressed in the distribution of relative lengths of articular processes, and the relatively large size of the (particularly caudal) lumbar vertebral bodies. These are well adapted to resist peak loads and shock impacts resulting from running. The lumbar lordosis in modern humans has been shown to assist in the transformation of potential to kinetic energy e.g. (Gracovetsky, 1986). The functional lumbar lordosis (in contrast to the passive lordosis of e.g. bipedal Japanese macaques) of modern *Homo sapiens* is highly likely a later adaptation to running and long distance walking and probably emerges only in combination with modern *Homo* body proportions, adaptations to produce effective breathing mechanisms, and barrel-shaped thorax and trunk rotation. Therefore, the lordosis observed in australopithecines is probably passive. Further, the arrangement of trunk muscles as extrapolated from the pelvis and sacrum indicates that the trunk stabilizers (*Quadratus lumborum*, *Obliquus externus* and *internus*) are not arranged in the same way as in modern humans. Thus, the likely lack of trunk rotation (requiring less flexibility) and smaller lateral trunk bending during locomotion require a less flexible australopithecine vertebral column. The climbing locomotor mode of *Australopithecus*, on the other hand could have benefited from the more restricted mobility of the lumbar spine. Since only a small degree of motion occurs in the spine during walking, mobility of the lumbar spine is important only during running where momentum and force impact are considerably larger. Finally, the flexible lumbar spine of modern humans allows for better stabilization of angular momentum during running (Bramble and Lieberman, 2004).

In australopithecines on the other hand, several of these adaptations are not present: The vertebral bodies are relatively small and although this is no real bar to successful bipedal walking, it is probably not favourable for running and high momentum resistance and shock absorption. The inferior articular processes of australopithecines are relatively longer than those of great apes but they are still relatively shorter than those of modern humans. In combination with the relatively massive superior articular processes and joint facets this would indicate that the australopithecine lumbar spine was not yet as flexible as that of modern humans. This can be seen as an adaptation to a more stable spine in arboreal locomotion and would not have hampered the australopithecine bipedal gait at walking speed. However, during running (particularly over long distances), control of momentum would have been less optimal.

In addition, Schmid (1991) concludes that the combination of an ape-like upper limb and trunk morphology hampers the free mobility of the descended shoulder, therefore, arm swinging – a necessary stabilizing component in running - was not possible for *A. afarensis*. Schmid therefore rules out human-style running for *A. afarensis*. The overall trunk shape, closely resembling that of apes, would not allow a decoupling of upper and lower limbs during running (as seen in modern humans). However, this is crucial in the control of angular momentum. Furthermore, the ape-like thorax does lack specialised adaptations to intensive breathing decoupled from locomotion cadence as seen in modern humans. This indicates a further restriction of human-like endurance running. Finally, similar conclusions, based on differences in overall body proportions between *Homo* and *Australopithecus* and human physiology have been drawn by Bramble and Lieberman (2004), Wang et al. (2004) and Carrier (1984).

Evidence from postcranial morphology (including the lumbar spine) strongly indicates that australopithecines are not adapted to endurance running. In contrast, their postcranium shows clear adaptations to arboreal locomotion and bipedal gait at walking speed. Results from the present study are not sufficient to estimate what percentage of the locomotor repertoire of *Australopithecus* consisted of arboreal locomotion. However, that the lumbar vertebrae of *Australopithecus* resemble *Pan and Pongo* to some degree indicates adaptations to arboreal locomotor modes.

6.3 Protocol for the analysis of future fossil hominin vertebral findings

This study has shown that the analysis of the complete vertebral form with geometric morphometric methods provides interesting results with regards to the comparison of fossil material with modern hominoids as well as other fossils. It allows the assessment of the complete vertebral form as well as a separate analysis of vertebral size and shape. Thus, a potential new fossil hominin vertebra could be analysed as follows:

- Landmarks are defined and sampled one the fossil (use definition of landmarks from table 2.6, p 111). If the fossil is fragmentary, the missing pieces need to be reconstructed first
- Landmark data from the fossil can then be analysed in comparison to modern hominoid taxa (for a copy of the modern hominoid data, contact the author at s.martelli@ucl.ac.uk)

- An easy way to analyse landmark data is the software morphologika, for a copy contact http://www.york.ac.uk/res/fme/resources/software.htm
- With regards to vertebral size, the comparison of the new fossil with modern hominoids can reveal whether the fossil has exceptionally large (or small) vertebrae relative to its estimated body weight and in comparison to the modern taxa. This can indicate whether the fossil had an orthograde or pronograde habitual trunk posture
- With regards to vertebral shape, the comparison of the new fossil with modern hominoids can reveal whether its locomotor repertoire contains considerable amounts of climbing and terrestrial quadrupedal gaits (it will cluster closest with the African apes), consists predominantly of climbing modes (it will cluster closest with *Pongo*) or if it relied on forms of bipedalism (it will gall closest to the modern human sample
- Assuming, the new fossil belongs to a fossil hominin (i.e. a new species of *Australopithecus* or *Paranthropus*), differences in vertebral size and shape between the fossil and modern humans could reveal further details about the bipedal gaits of this fossil. If the vertebra was larger than expected in relation to the estimated body weight of the fossil (and compared to modern great apes), this could be interpreted as an adaptation to large shock absorption due to high impact locomotor modes (such as running or maybe leaping). In vertebral shape, the presence of long inferior articular processes in combination with short superior ones (condition observed in *Homo*), short, horizontally orientated spinous processes, and a large *Incisura vertebralis major* are telltale signs of a flexible lumbar spine similar to modern humans. It could be concluded that the fossil in question was adapted to bipedal walking and long distance running. In case where the vertebral shape is similar to that of modern humans but transgresses in details such as the length of the articular processes or the overall size of the vertebrae, alternative bipedal locomotor modes (i.e. no long distance running) and compromises with other locomotor modes (i.e. climbing modes) should be considered

6.4 Future outlook

Future studies could benefit from more detailed analyses of the ontogeny of vertebral form using decent samples. Such analyses could provide better insights into the extent

to which features develop secondarily to functions (i.e. loading) or primarily under the control of genetic systems. Particularly valuable would be experimental ontogenetic studies in which alterations of loading (e.g. trained macaques) are fully related to the development of form.

Additionally the findings of this study point to the ways in which the morphology of the spine is linked to that of the pelvis and thorax. It would be of interest to examine covariations between these structures in order to gain insights into the developmental and evolutionary mechanisms that that underpin the integration of these components.

The present study focused on the external shape of lumbar vertebrae. Recent studies of internal bone structures (e.g. patterns of trabecular structures) have shown that these analyses can yield valuable insight into the loading patterns of a particular skeletal part (Brown et al., 2002; Macchiarelli et al., 1999; MacLatchy and Muller, 2002; Oxnard, 1983; Pal, 1989; Roy et al., 1999). The comparison of australopithecine trabecular patterns with those of modern hominoid taxa might help to further resolve the nature of the arboreal locomotor modes in the australopithecine locomotor repertoire.

6.5 Summary of findings and interpretations

The present study set out to investigate the variation in vertebral size and shape within and between modern hominoid taxa and fossil hominins. The variation in size and shape observed within and between modern hominoid taxa was investigated in relation to differences (intra-and inter-specific) in locomotor repertoires, body weight, and phylogeny. The variation in vertebral size and shape within fossil hominins and between fossil hominins and modern hominoid taxa was explored in relation to differences in locomotor repertoires. The main results of the study can be summarized as follows:

With regard to aims 1 to 4 (Intra-specific vertebral size and shape variation in modern hominoid taxa) this study concludes that

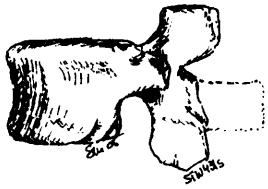
1. In all great ape taxa, differences in body weight have the largest impact on sexual dimorphism in vertebral size and shape
2. In modern humans, differences in vertebral shape and metameric patterns of size variation are also related to sexual dimorphism in pelvic morphology

With regard to aims 5 to 7 (inter-specific vertebral size and shape variation in modern hominoid taxa) this study concludes that

1. Of the three factors (body weight differences, differences in locomotor repertoires, and phylogeny) investigated in relation to vertebral size and shape, differences in locomotor repertoires have the most significant relationship with inter-specific vertebral shape variation. Differences in vertebral size are partially influenced by differences in body weight and to a small extent (humans vs. great apes) by differences in locomotor repertoires
2. Phylogenetic history does not have a significant relationship with vertebral size and shape variation

With regard to aims 8 to 10 (fossil hominin vertebral size and shape variation) this study concludes that

1. Lumbar vertebral size and shape variation are very similar between the australopithecine taxa
2. *Australopithecus* shows a mix of human-like, ape-like and unique australopithecine anatomical features in lumbar spine morphology which indicates adaptation to arboreal and bipedal terrestrial locomotion
3. The australopithecine lumbar spine does not show adaptations to bipedal running and long distance travelling



APPENDIX

Illustrations of fossil vertebral material and reconstructions thereof, utilized in the present study

The following appendix contains a collection of illustrations of each of the fossil hominin vertebrae measured and employed in the present study. Vertebrae are not scaled relative to each other; neither are they shown in natural size. The illustrations are organized according to taxon. Pictures – where not indicated otherwise – are from the personal collection of the author (who is much indebted to Beverly Kramer, University of the Witwatersrand, Johannesburg and Frances Thackeray from the Transvaal Museum, Pretoria for the permission to take photographs of the original *A. africanus* fossil material.

In the case of *A. afarensis*, the single available vertebra is shown with and without the reconstructions. Pictures of specimen *A. africanus* Sts14 are from the original fossils and illustrate reconstructions applied to it directly by Robinson. The reconstructions of Sts14 vertebrae from CT scans are also shown. Of the *A. africanus* specimens Stw431, Stw572, and Stw8 pictures of casts only are shown. These illustrate the temporary reconstructions of missing vertebral elements made of plasticine and Bostik Blu-Tack® and were carried out by the author. The same applies for the *Homo ergaster* specimen KNM-WT 15000, with the exception of its last lumbar which was complete enough not to require any reconstructions.

*Australopithecus afarensis*AL288-1

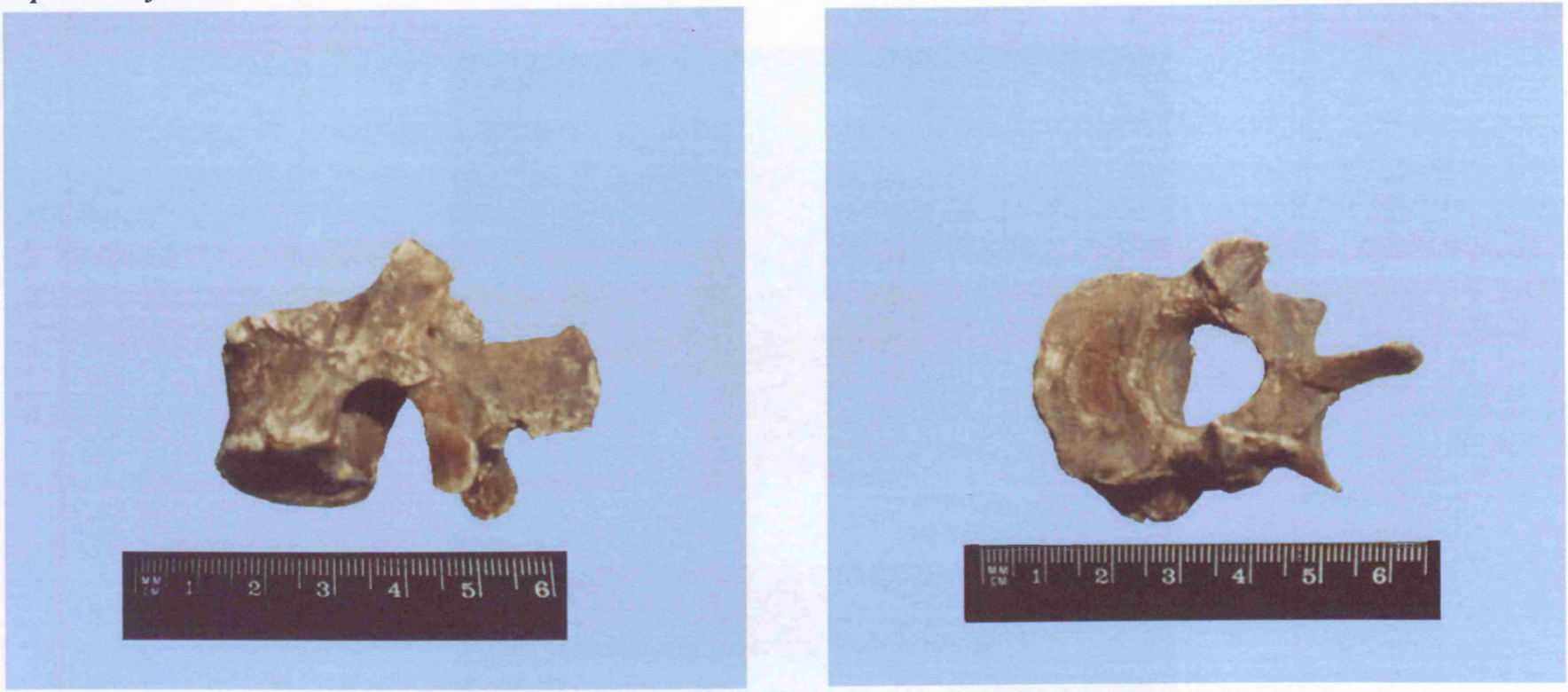


Figure A.1 Left lateral (left) and superior (right) view of cast of L3 (?), 288-1 *A. afarensis.* Reconstruction of original vertebra by Johanson et al (1982). Cast material epoxy, cast made from the original bone material. Original at the National Museum in Addis Abbeba, Ethiopia

***Australopithecus afarensis*AL288-1**

Figure A.2 Posterior view of cast of L3 (?), 288-1 *A. afarensis*. Reconstruction of original vertebra by Johanson et al (1982), reconstruction of costal processes on cast by author. Cast material epoxy, cast made from the original bone material. Original at the National Museum in Addis Abbeba, Ethiopia

Australopithecus africanus

Sts14 reconstructions

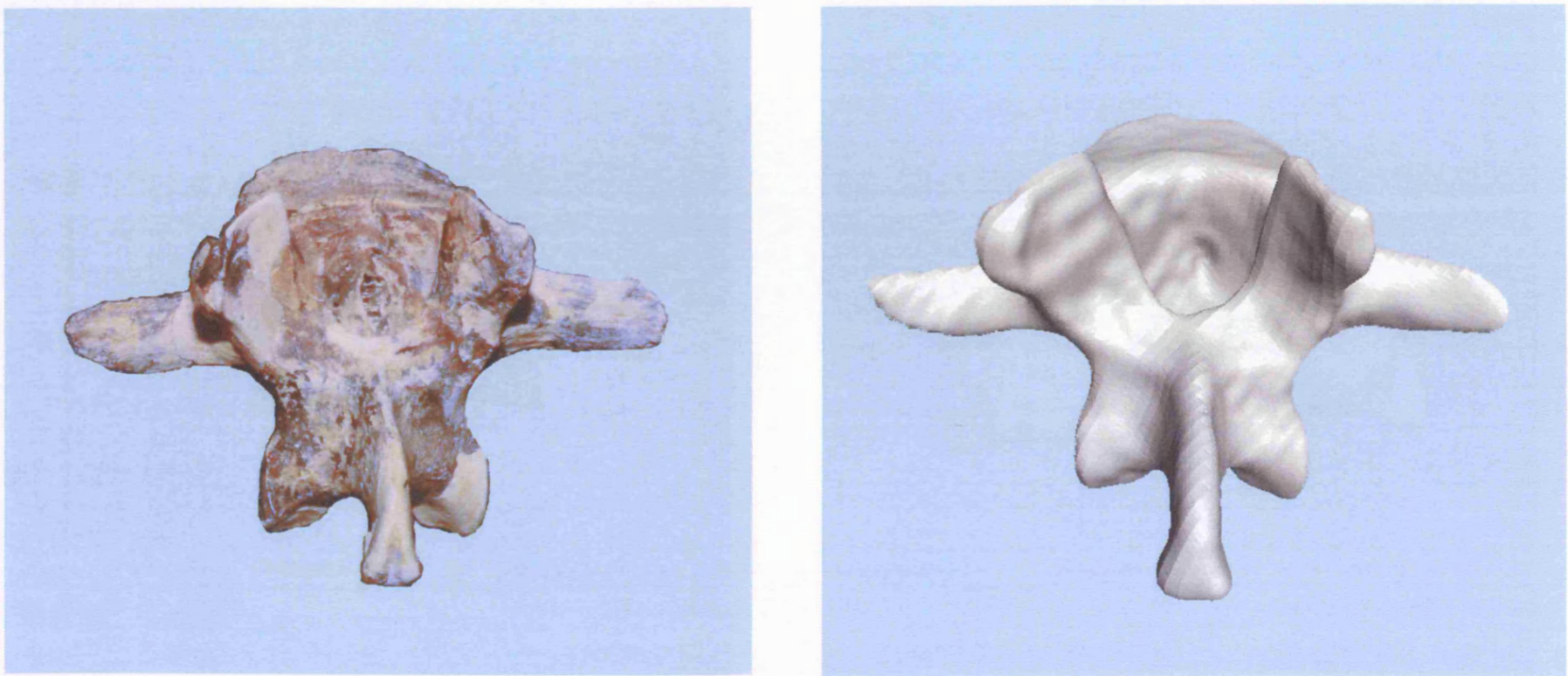


Figure A3 Posterior view of original fossil (left) and of CT scan reconstruction (by the author) with landmarks (right) of L1 Sts14e *A. africanus*. Note light coloured, reconstructions (material gypsum) of left superior and right inferior articular processes as well as of spinous process applied to original fossil by Robinson (1972). Original at the Transvaal Museum, Pretoria, South Africa

Australopithecus africanus

Sts14 reconstructions

Figure A4 Left lateral view of original fossil (left) and of CT scan reconstruction (by the author) (right) of L2 Sts14d *A. africanus*. Original at the Transvaal Museum, Pretoria, South Africa

Australopithecus africanus
Sts14 reconstructions

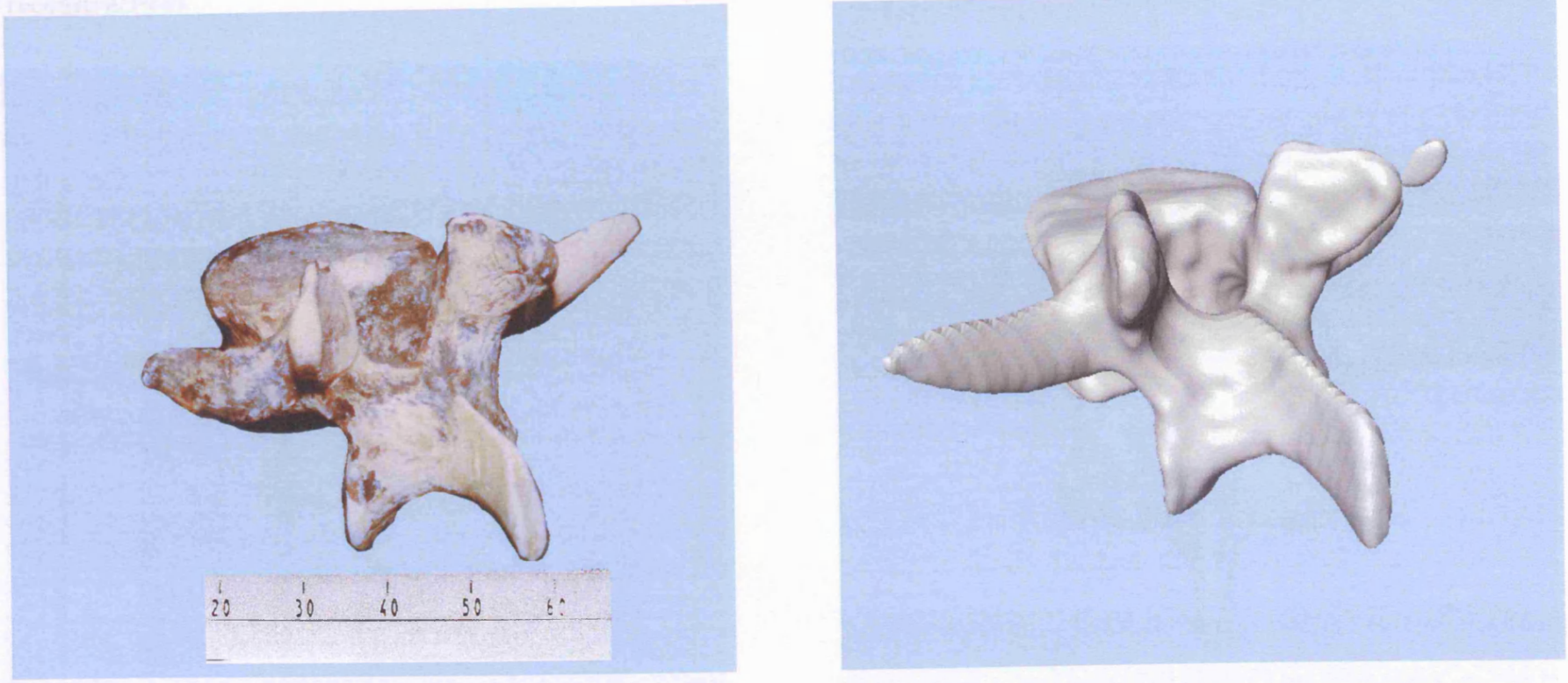


Figure A5 Left latero-posterior view of original fossil (left) and of CT scan reconstruction (by the author) (right) of L3 Sts14c *A. africanus*. Note light coloured reconstructions (material gypsum) of vertebral arch, right costal process, left superior and inferior articular process, and spinous process applied to original fossil by Robinson (1972). Also note damage to vertebral body (right half) visible in original fossil and reconstructed in the CT scan reconstruction with amira™ (by the author). Original at the Transvaal Museum, Pretoria, South Africa

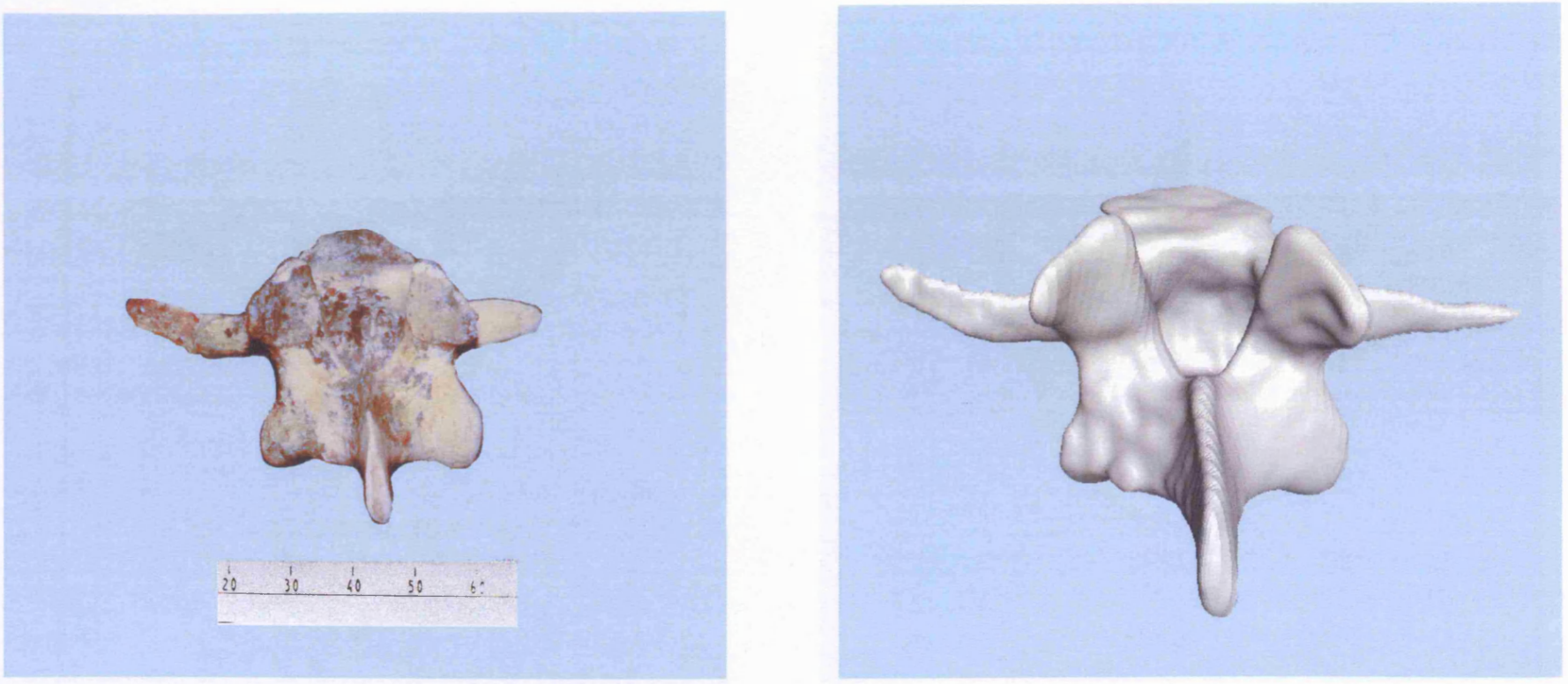


Figure A.6 Posterior view of original fossil (left) and of CT scan reconstruction (by the author) (right) of L4 Sts14b *A. africanus*. Note light coloured, reconstructions (material gypsum) of vertebral arch, right costal process, right superior and inferior articular processes, and spinous process applied to original fossil by Robinson (1972). Also note damage to vertebral body visible in original fossil and its reconstruction as well as additional reconstruction of right costal process in the CT scan reconstruction, produced with amira™ (by the author). Original at the Transvaal Museum, Pretoria, South Africa

Australopithecus africanus

Sts14 reconstructions

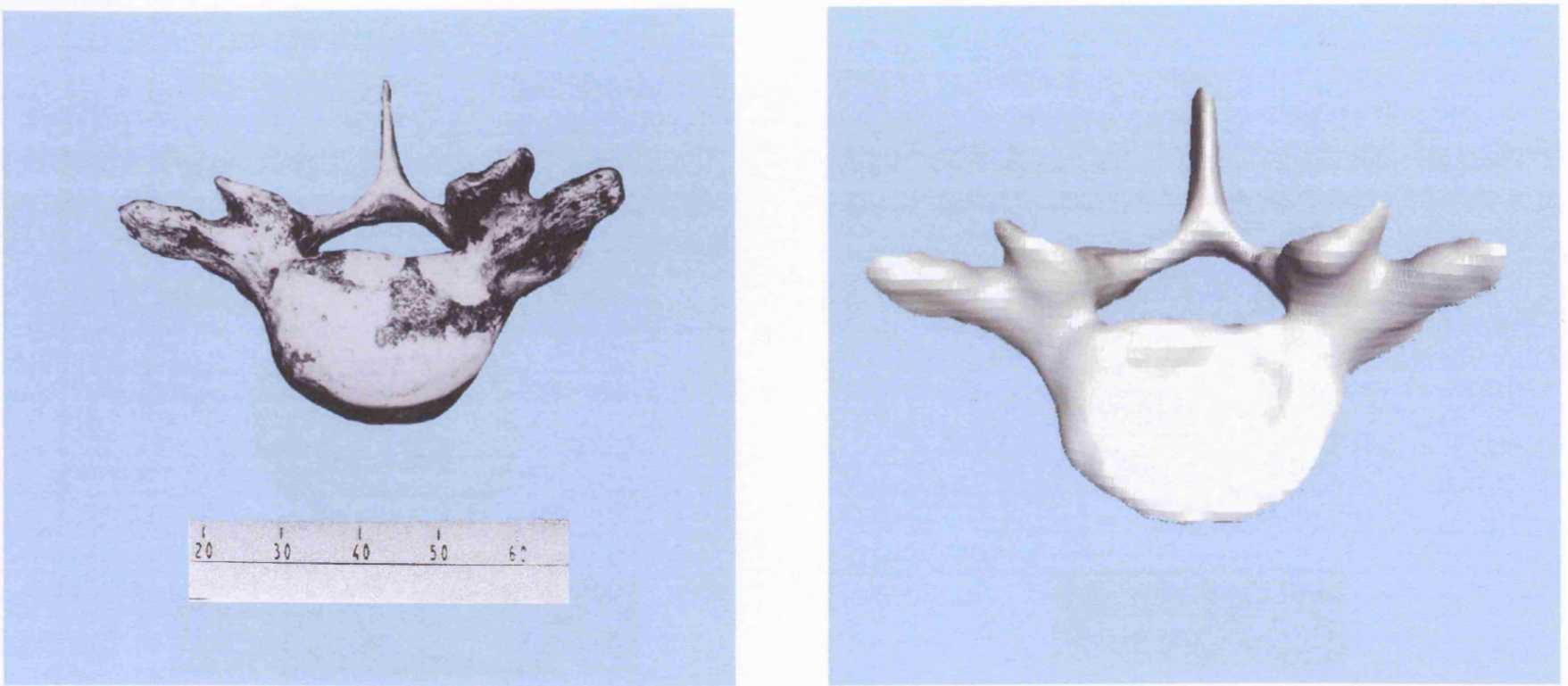


Figure A.7 Superior view of original fossil (left) and of CT scan reconstruction (by the author) (right) of L5 Sts14a *A. africanus*. Note light coloured, extensive reconstruction (material gypsum) of vertebral body and spinous process applied to original fossil by Robinson (1972). Original at the Transvaal Museum, Pretoria, South Africa

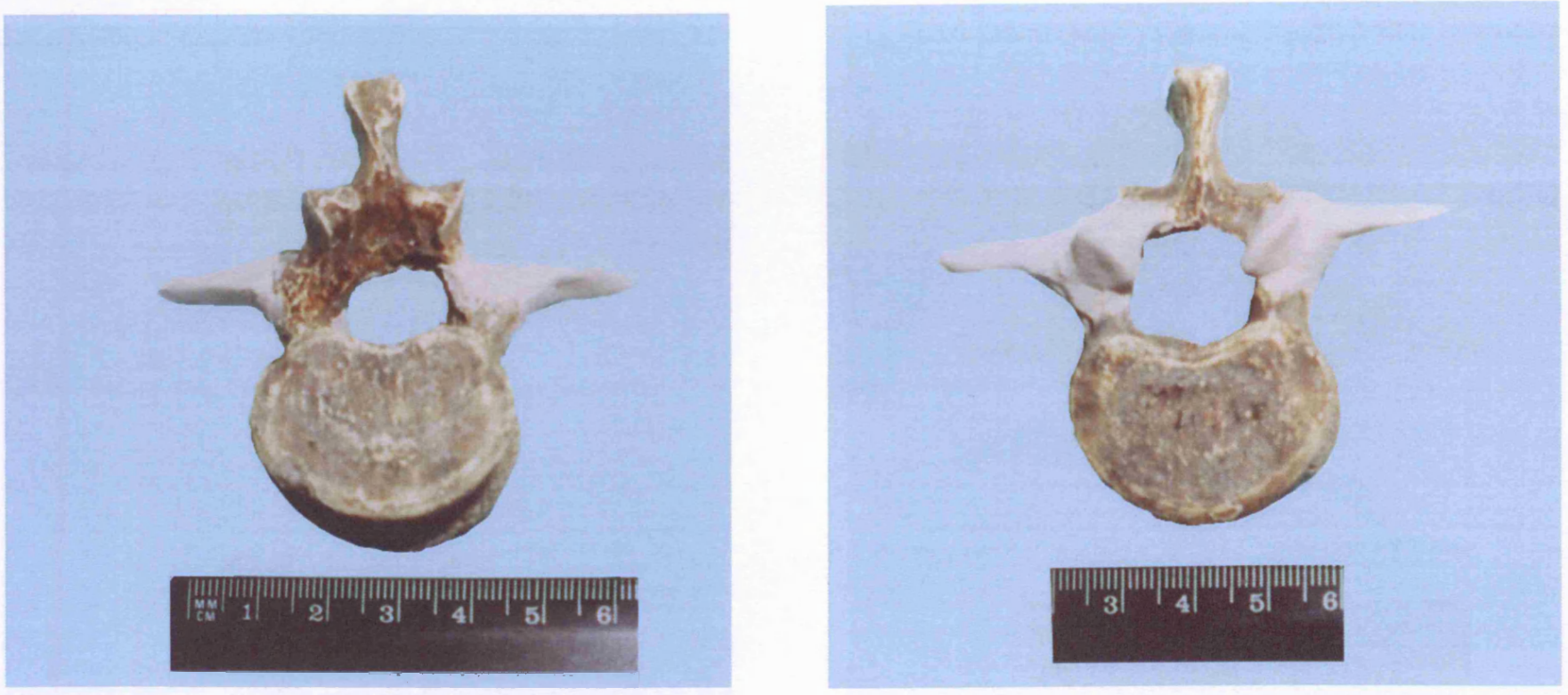


Figure A.8 Inferior (left) and superior (right) view of cast of L1 Stw431r, qa/ab, *A. africanus*. Costal processes, superior articular processes, and pedicles partially reconstructed (by the author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Australopithecus africanus

Stw431 Reconstructions

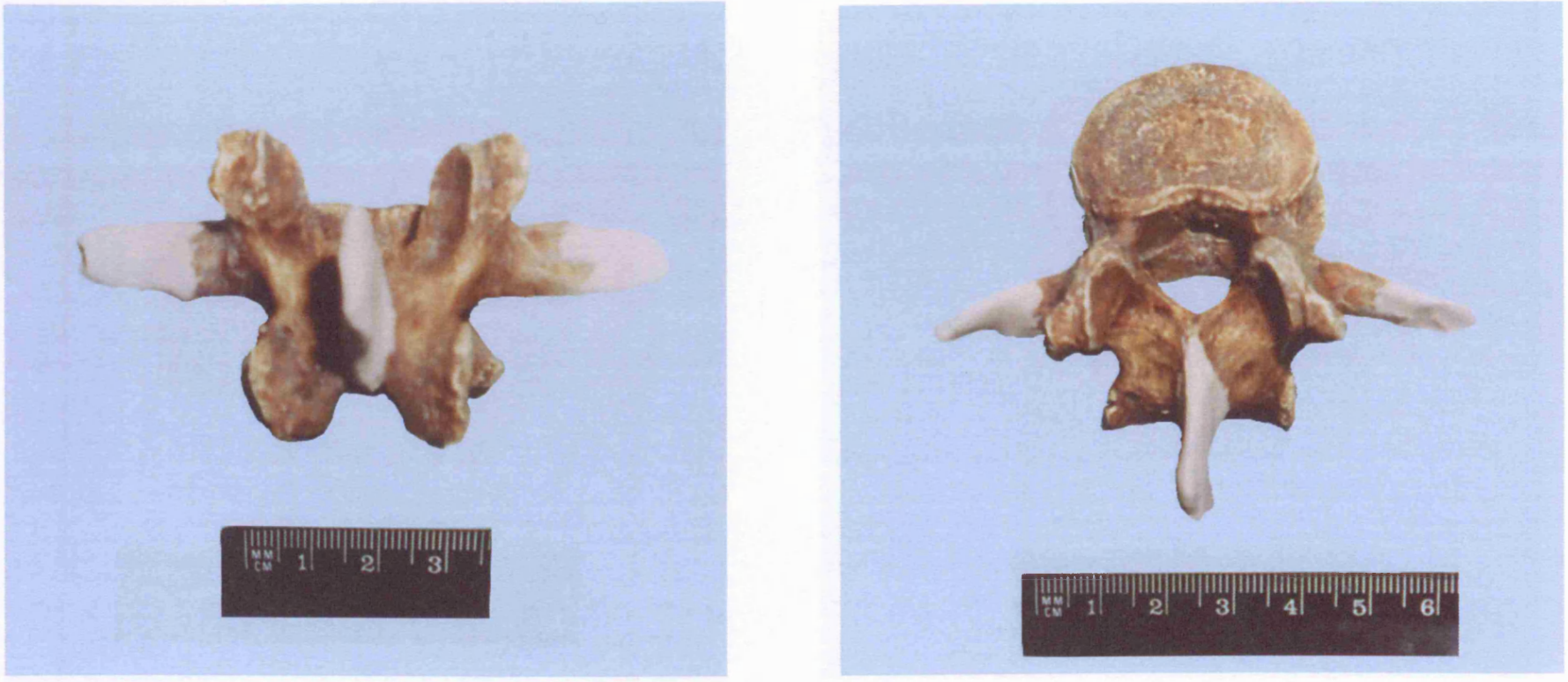


Figure A.9 Posterior (left) and postero-superior (right) view of cast of L2 Stw431s, *A. africanus*. Costal processes and spinous process partially reconstructed (by the author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Australopithecus africanus

Stw431 Reconstructions

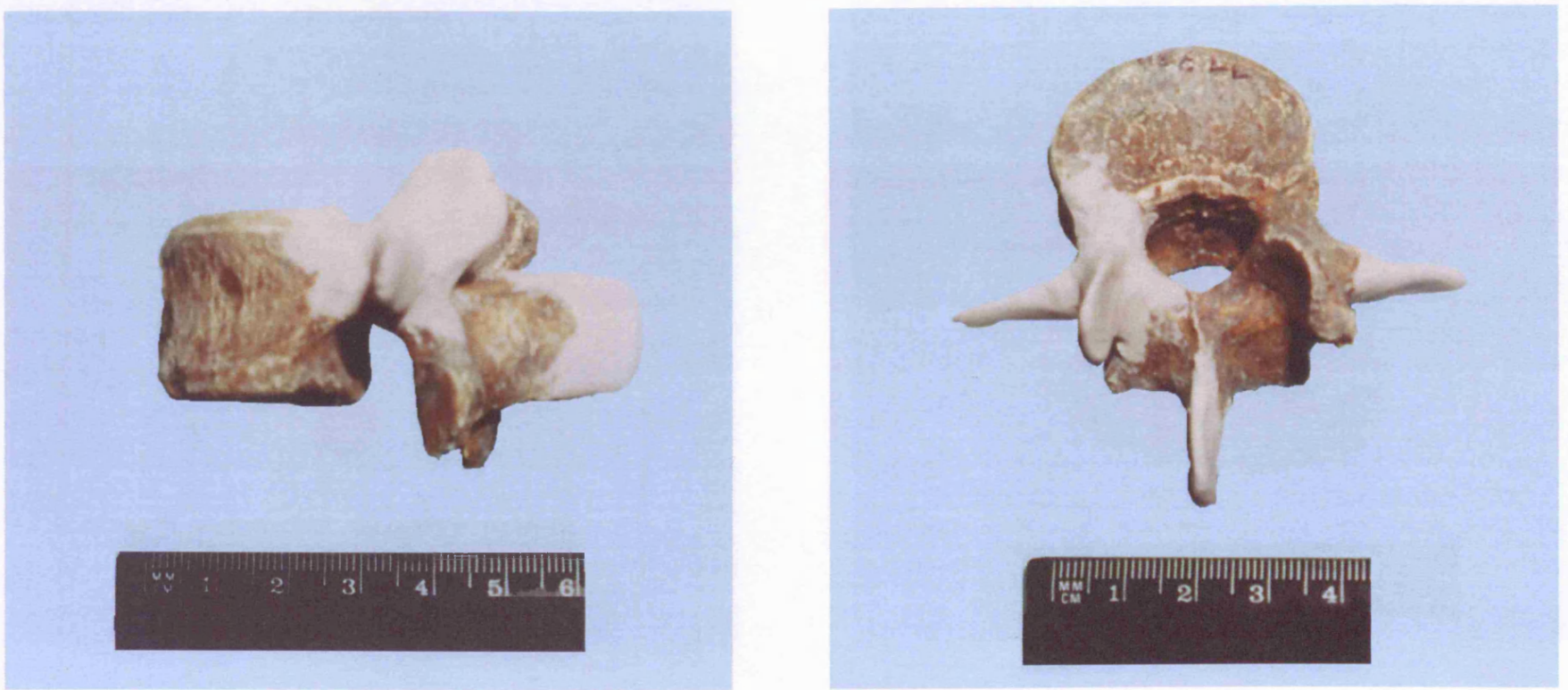


Figure A.10 Left lateral (left) and postero-superior (right) view of cast of L3 Stw431t, *A. africanus*. Costal processes, left pedicle, left superior articular processes, left superior vertebral body endplate well as partial spinous process reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

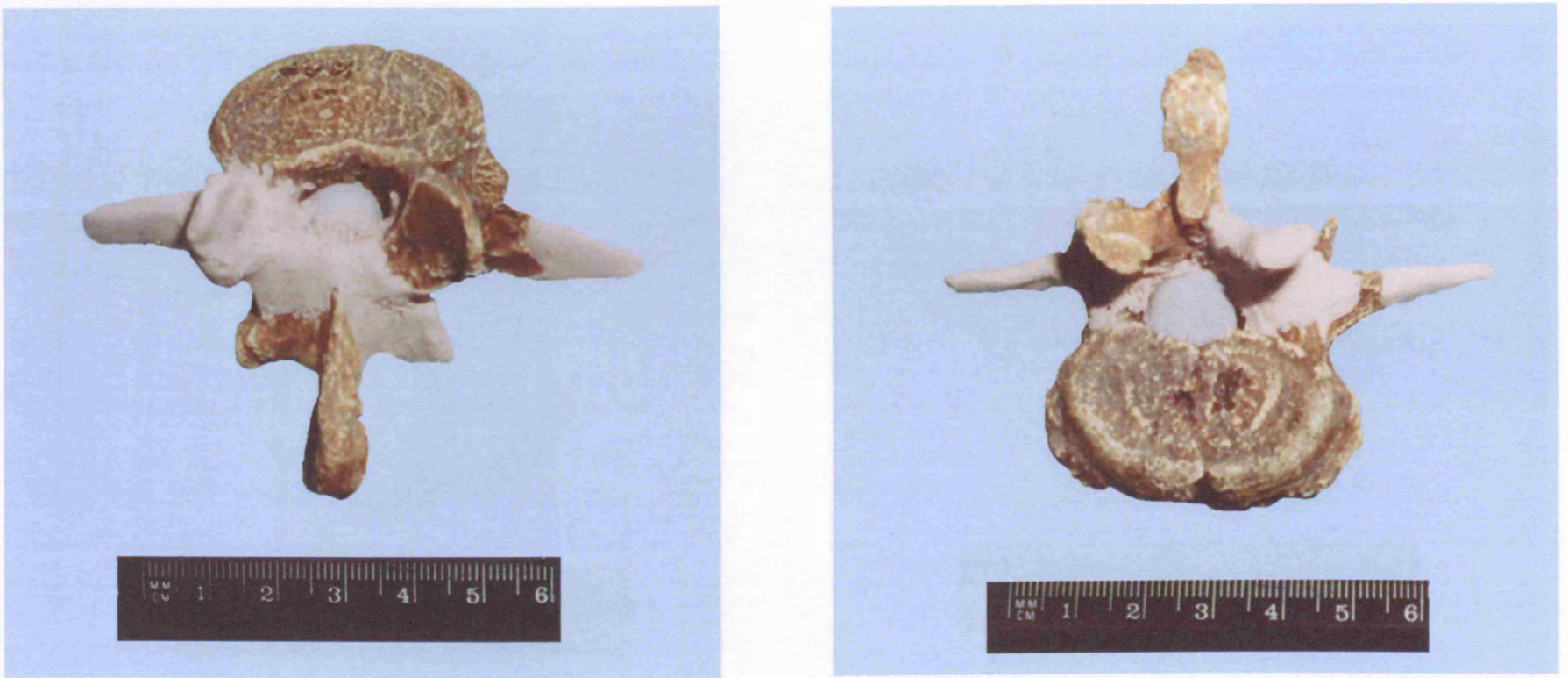


Figure A.11 Postero-superior (left) and inferior (right) view of cast of L4 Stw431u, *A. africanus*. Right inferior and left superior articular processes fully and costal processes, pedicles, and vertebral arch partially reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Australopithecus africanus

Stw431 Reconstructions

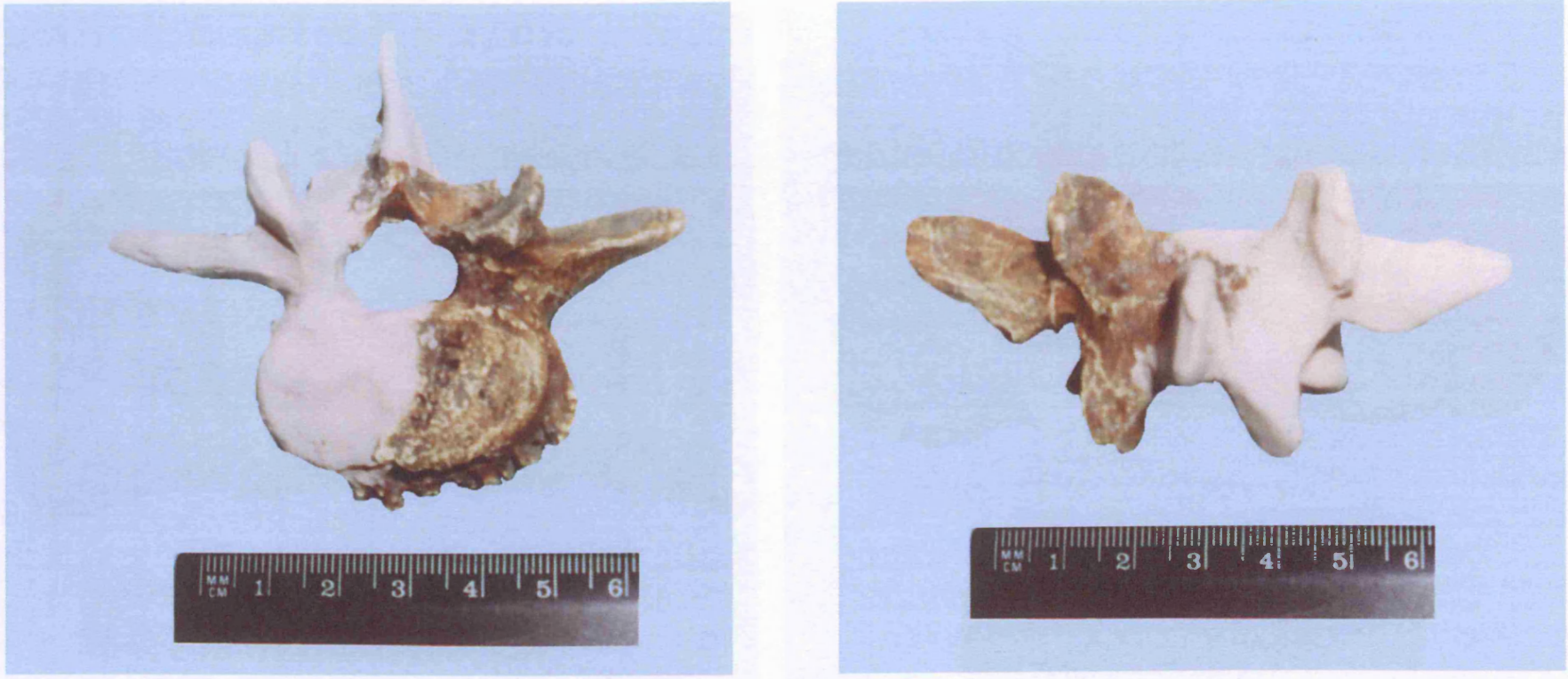


Figure A.12 Superior (left) and posterior (right) view of cast of L5 Stw431v, *A. africanus*. Right half and spinous process reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Australopithecus africanus

Stw8 Reconstruction

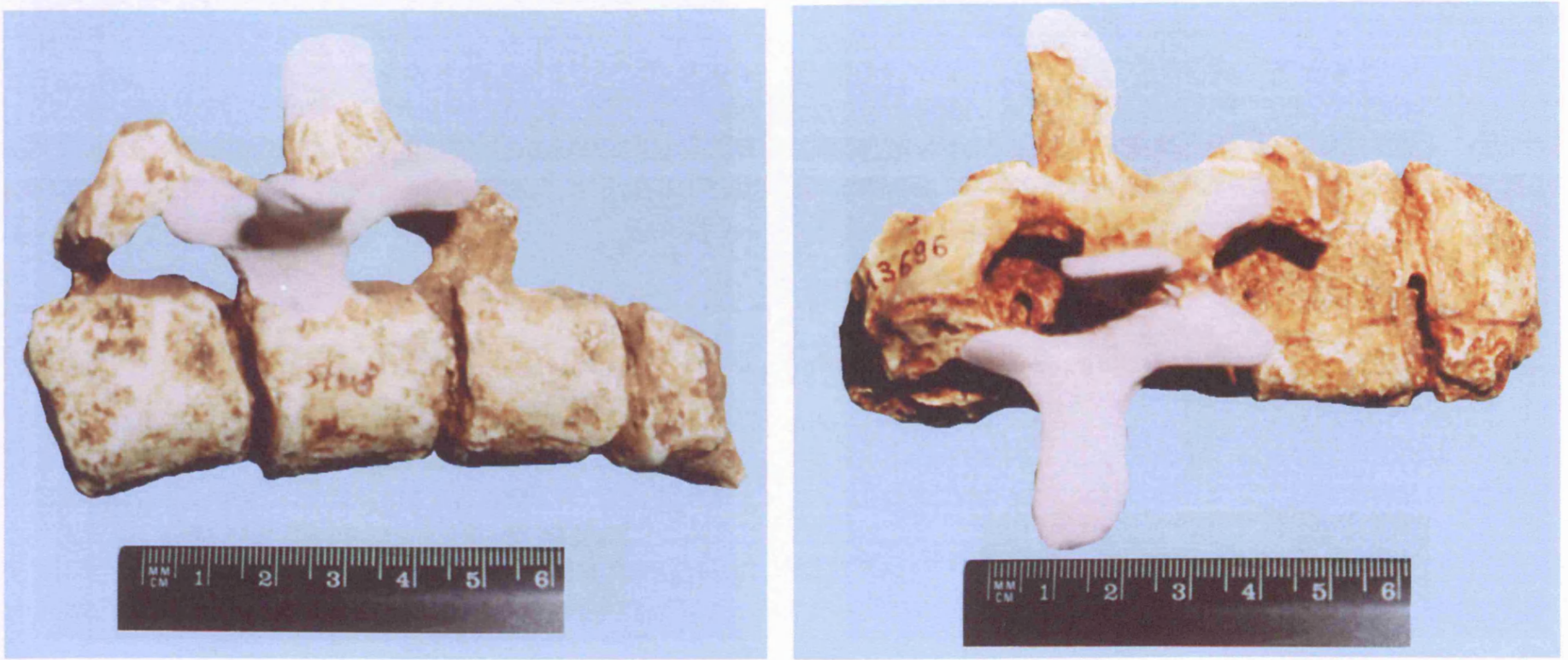


Figure A.13 Left lateral (left) and superior (right) views of cast of L1 (?) to L4 (?) lumbar series, Stw8, *A. africanus*. Left pedicle, left superior and inferior articular processes, costal processes, and partial spinous process reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Australopithecus africanus

Stw572Reconstruction

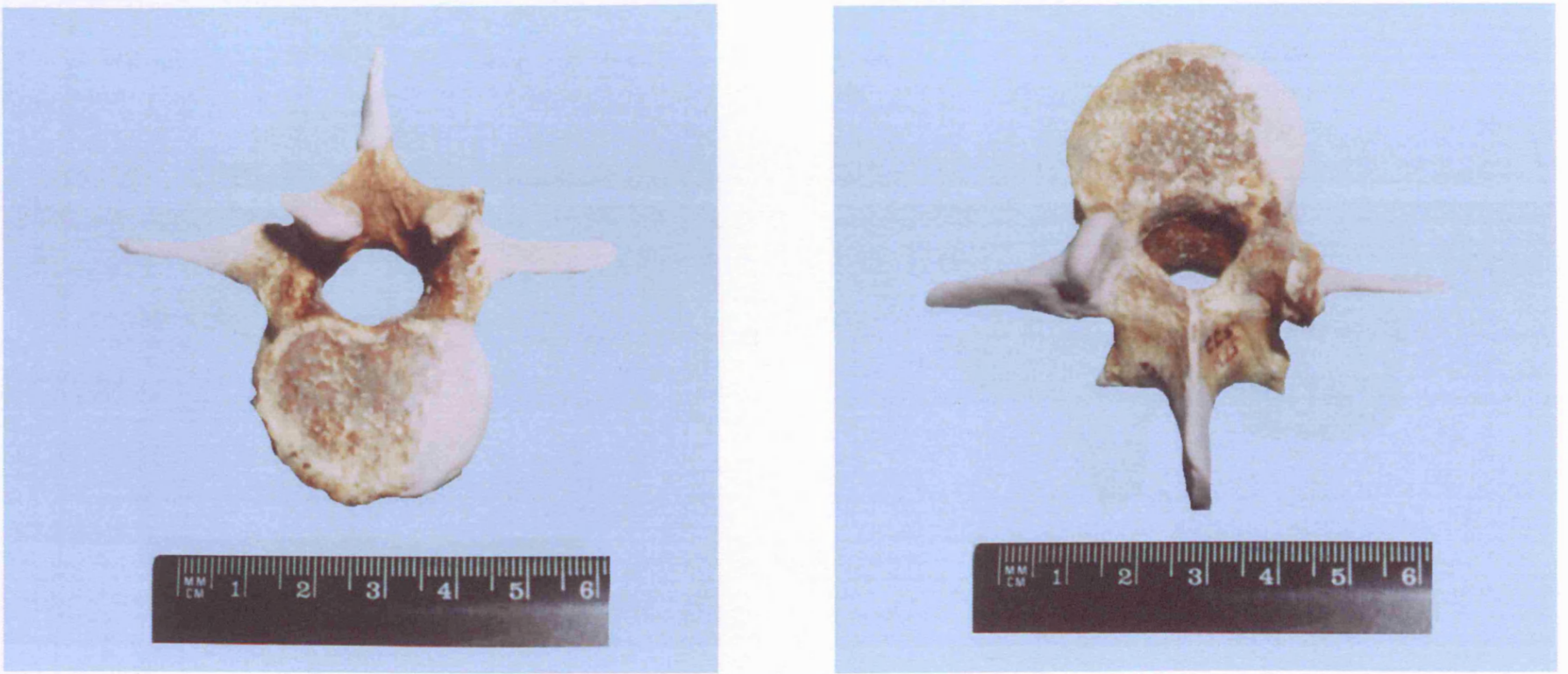


Figure A.14 Inferior (left) and postero-superior (right) view of cast of L4 (?) Stw572, *A. africanus*. Right rim vertebral body, spinous process, costal sprocess, left inferior and superior articular processes reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the University of the Witwatersrand, Johannesburg, South Africa

Homo ergaster

KNM-WT 15000 Reconstructions

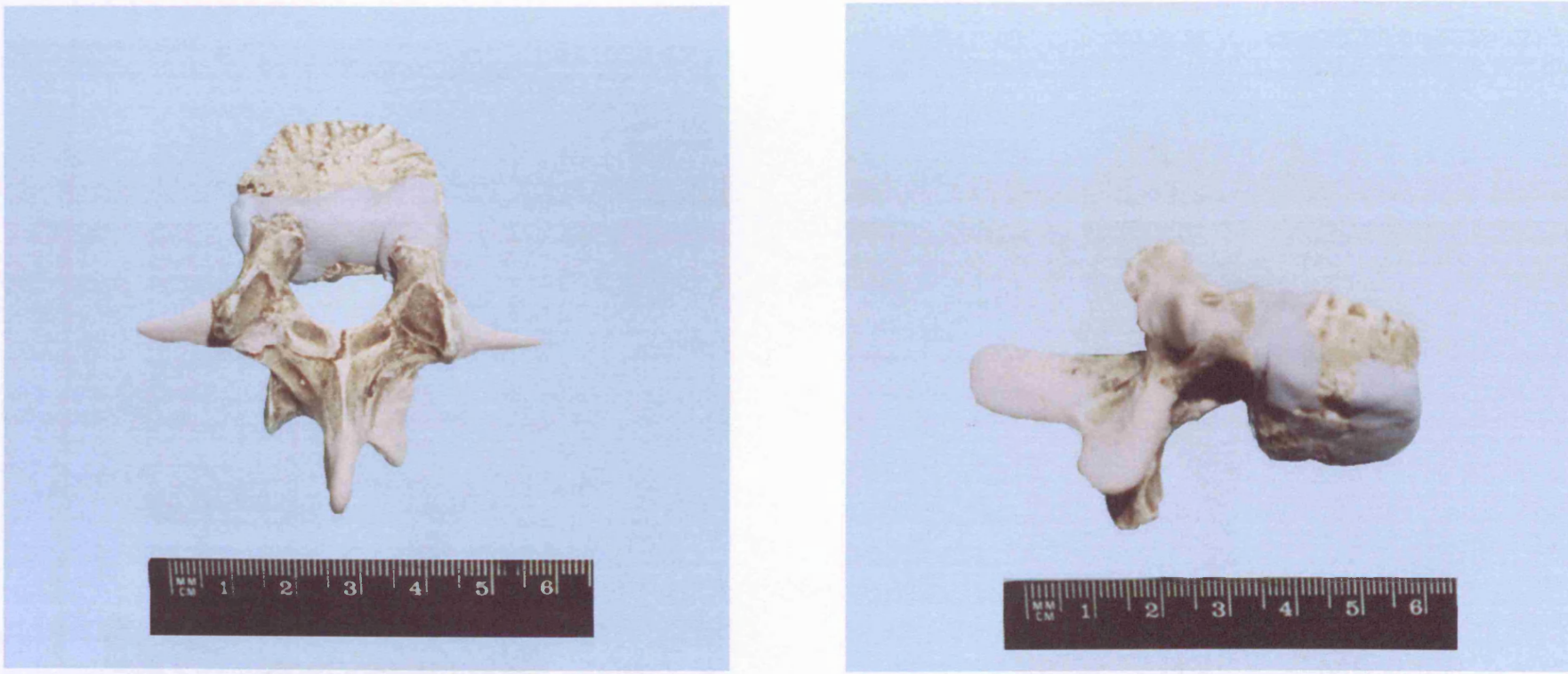


Figure A.15 Superior (left) view and right infero-lateral (right) view of cast of L1 KNM-WT 15000AV/AA, *Homo ergaster*. Posterior and infero-anterior part of vertebral body, costal processes, inferior articular process and partial spinous process reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the Kenya National Museum, Nairobi, Kenya

Homo ergaster

KNM-WT 15000 Reconstructions

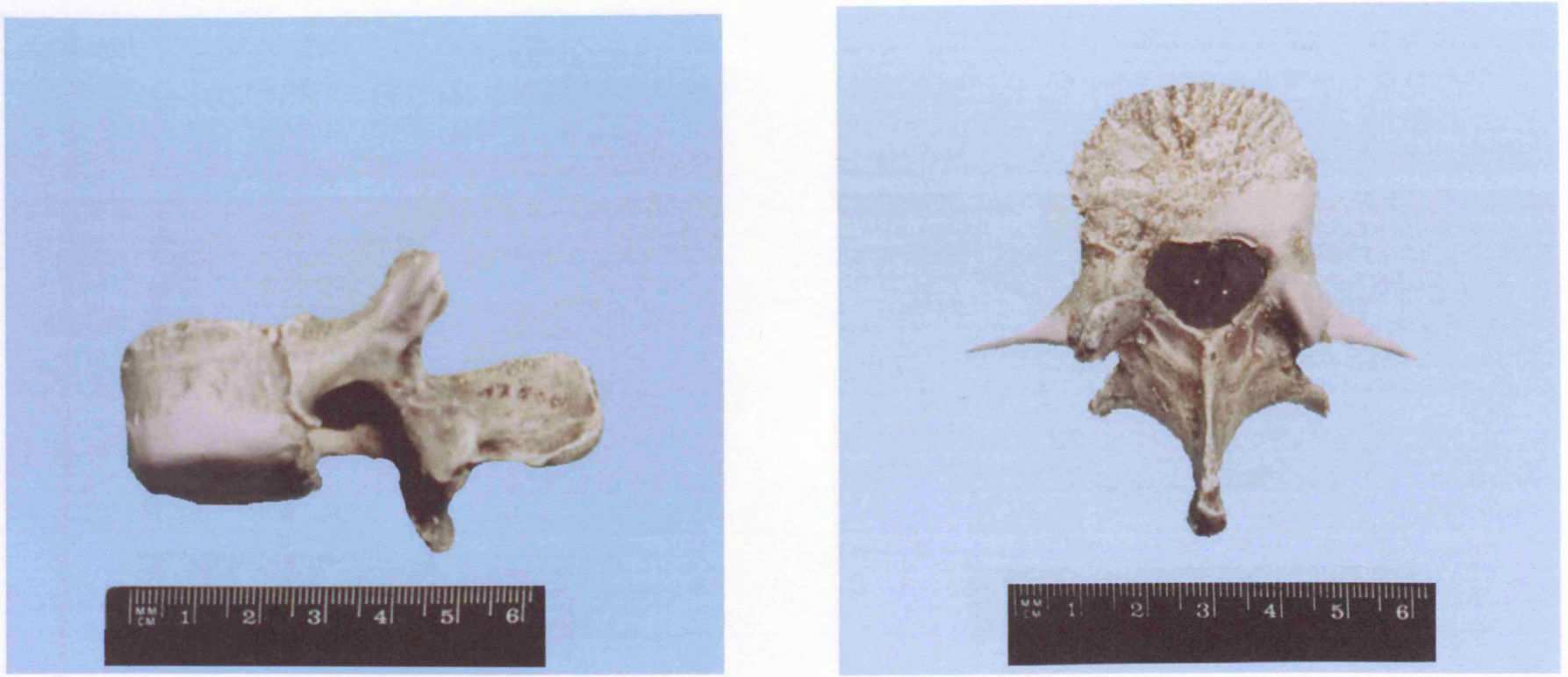


Figure A.16 Left infero-lateral (left) view and superior (right) view of cast of L3 KNM-WT 15000AB, *Homo ergaster*. Inferior part and right posterior part of vertebral body, right superior articular process and costal processes reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the Kenya National Museum, Nairobi, Kenya

Homo ergaster

KNM-WT 15000 Reconstructions

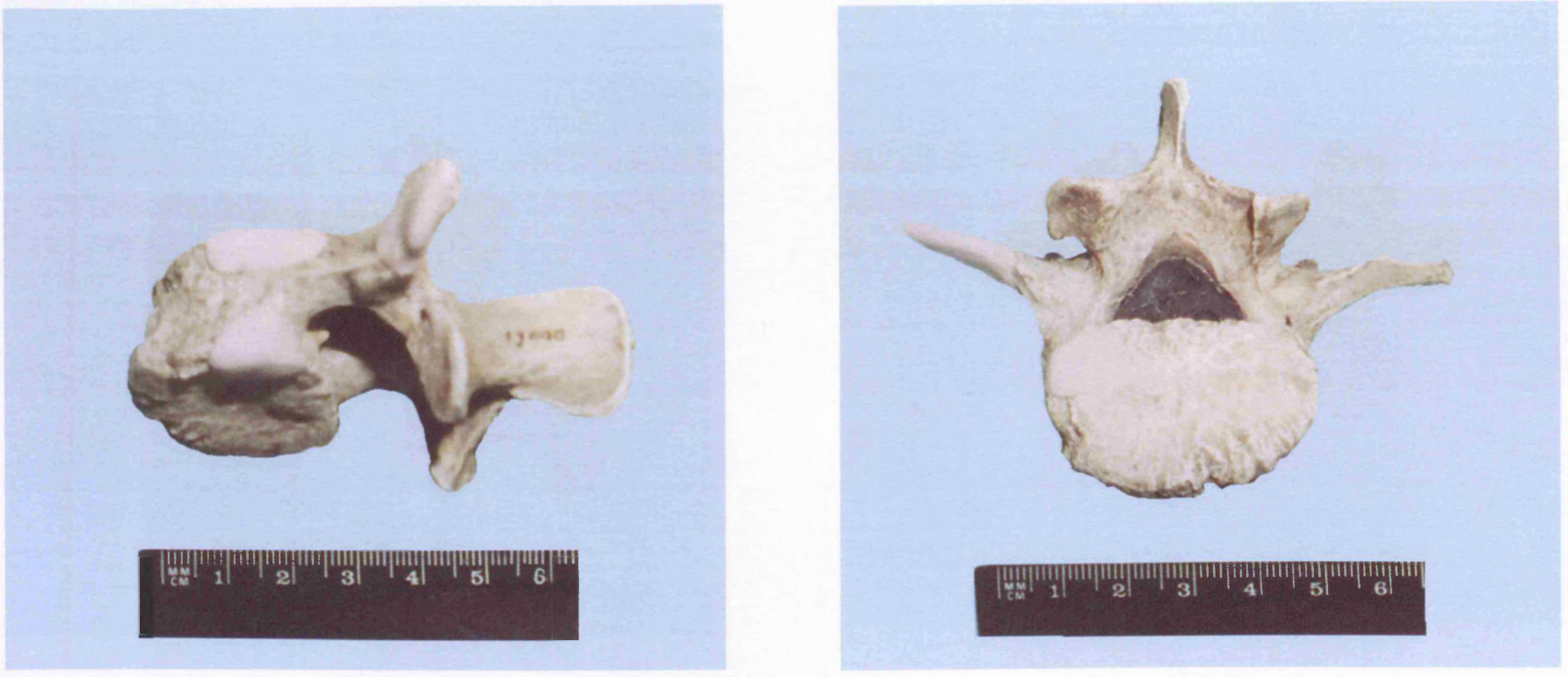


Figure A.17 Left infero-lateral (left) and inferior (right) view of cast of L4 KNM-WT 15000 BM, *Homo ergaster*. Inferior and superior rim of vertebral body, left costal process reconstructed (by author). Cast material epoxy, casts made from the original fossils. Original at the Kenya National Museum, Nairobi, Kenya

Homo ergaster

KNM-WT 15000 Reconstructions

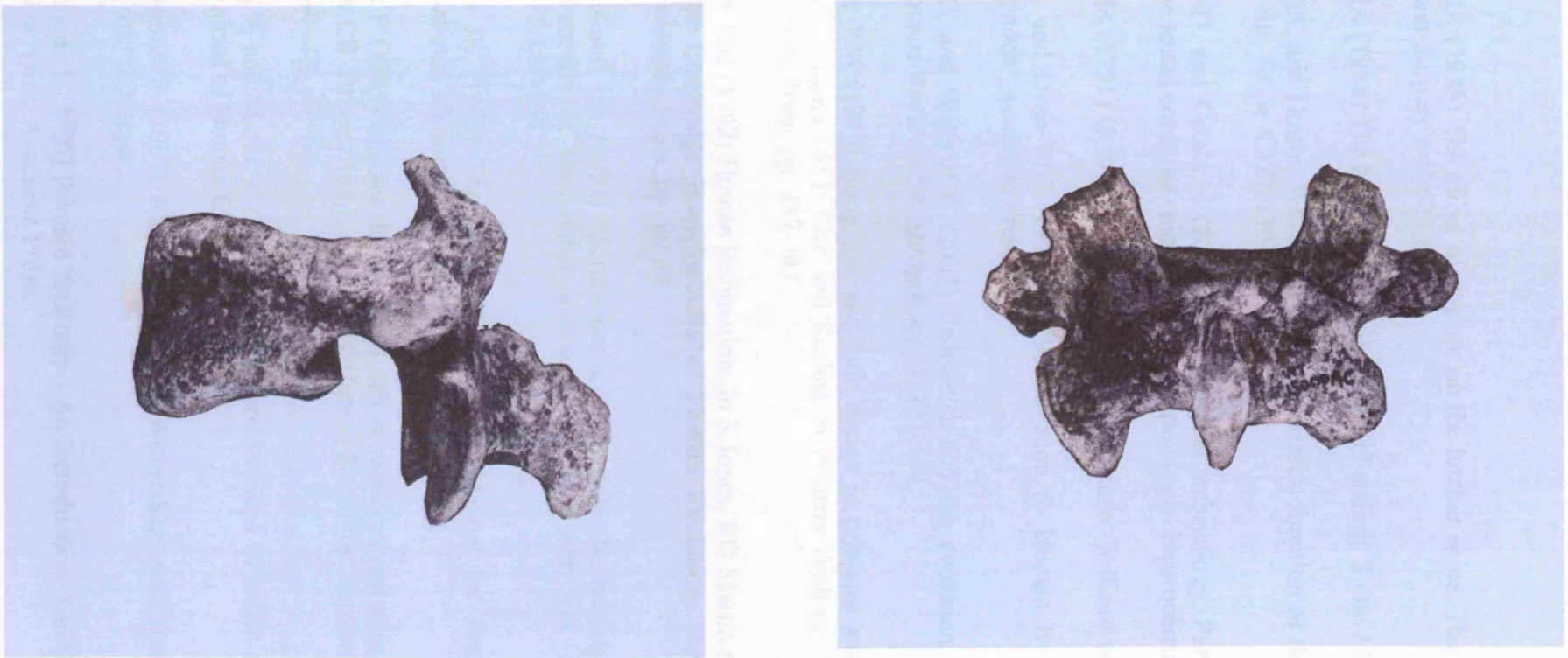


Figure A.18 Left lateral (left) and posterior (right) view of original fossil, L5 KNM-WT 15000AC, *Homo ergaster*, from Walker and Leakey (1993), p115; natural size. No reconstruction needed. Cast material epoxy, casts made from the original fossils. Original at the Kenya National Museum, Nairobi, Kenya

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